Transport and retention of benthic marine invertebrates in the Southern Tauranga Basin

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Abstract

Dispersal is the process in which individuals are transferred between populations, and is essential for population sustainability and longevity. In estuarine soft sediment communities, dispersal often occurs as the interaction between the individual and tidal flows. Many coastal benthic marine invertebrate populations have been considered open because of the dispersal potential of a pelagic larval phase, with populations maintained by an external supply of recruits. However, for estuarine populations, recent evidence has suggested that populations may be more closed because of local hydrodynamic conditions causing larval retention within the source estuary. In this thesis, field observations and numerical simulations were used to investigate the effect of estuary morphology on the transport and retention of benthic invertebrate larvae in Tauranga Harbour, a large (218 km^2), shallow (mean depth = 2.8 m) meso-tidal estuary. Previous studies indicate that residence times extracted from hydrodynamic modelling vary throughout the harbour, due to residual circulation patterns caused by complex channel morphology. Field observations indicate increased abundance and differing community composition of invertebrate larvae in the upper harbour compared to the lower. Tidal circulation is asymmetrical, with transport through a seaward channel during flood tides, and in a landward channel during ebb, suggesting that larval retention in the upper harbour may provide a source of larvae for the lower harbour. Larval transport pathways were evaluated by a coupled hydrodynamic-transport model and confirmed those observed in the field. Modelled larvae, released under different stages of spring-neap tidal cycle in the upper harbour, were retained for up to 16 d whereas retention for larvae released in other harbour locations was much more variable and depended on the timing of release and direction of initial transport. Results of this study highlight the impact of complex channel morphology (particularly at a scale of 10s to 100s of meters) on the large scale circulation and subsequent transport and retention of benthic invertebrate larvae. Understanding these influences on the transportation of benthic invertebrate larvae and the identification of retentive regions, will aid future population management or conservation efforts

Preface

This thesis comprises of two research chapters, Chapter 2 describes the development of a coupled hydrodynamic-transport model to study larval dispersal, and Chapter 3 applies this model to aid field data analysis and was submitted for peer review in *Journal of Marine Systems*. I was responsible for data analysis, numerical modelling and writing of this thesis. Apart from where explicitly referenced this work is from my own ideas and was completed under the supervision of Professor Conrad Pilditch, Associate Professor Karin Bryan and Dr Julia Mullarney from the University of Waikato, with further support from Dr Niall Broekhuizen from the National Institute of Water and Atmospheric Research Ltd (NIWA).

Chapter 3 was submitted for peer review to *Journal of Marine Systems* with the title 'Transport and retention of benthic marine invertebrates in a large semi-enclosed meso-tidal coastal lagoon' by Bradley J. Monahan, Conrad A. Pilditch, Karin R. Bryan, Niall Broekhuizen, Joanne I. Ellis.

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Chapter 1. General introduction

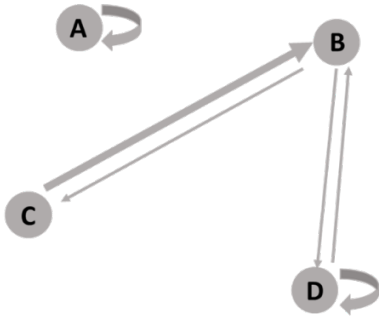
1.1. Population connectivity

Dispersal is an essential process for the sustainability and longevity of populations in both aquatic and terrestrial environments (Kokko & López-Sepulcre, 2006). This process allows for the transfer and import of new individuals to populations in different locations; and is essentially the movement of individuals from birth to the location of breeding (Kokko & López-Sepulcre, 2006). The transfer of individuals between populations encourages genetic variation, allowing for adaptation to environmental changes (Bohonak, 1999). Dispersal and recruitment of individuals is also of significance for population persistence. Maintaining multiple populations within a region ensures that if a single population is lost (potentially due to an unsuitable habitat), the entire local species (meta-population) does not become extinct (Hanski & Gilpin 1991, Cowen & Sponaugle, 2009, Nickols et al. 2015).

Marine ecologists are often interested in where individuals disperse to, and which populations are connected or fragmented within a meta-population. Population connectivity refers to the recruitment of individuals from geographically-separate populations of the same species (Gawarkiewicz et al. 2007, Pineda et al. 2007). Populations in which connectivity is high (in terms of both transfer direction and magnitude; e.g. transfer to Population B from C and D, Figure 1-1) are generally better equipped to respond to environmental change. However, populations which are highly fragmented or self-seeding (self-recruiting) are at higher risk of population losses (e.g. Population A, Figure 1-1). The meta-population concept refers to a population of populations within a given location, which occupy distinct habitat patches (Roughgarden & Iwasa, 1986, Hanski & Gilpin, 1991, Cowen & Sponaugle, 2009, Nickols et al. 2015).

Globally, marine ecosystems are under increased anthropogenic pressures (Jackson et al. 2001, Kemp et al. 2005, Levin 2006, Cowen & Sponaugle 2009). Estuaries have received intensive impacts due to land use change and intensification, land reclamation, dredging and increased shipping traffic (Kenny & Rees, 1994, Jackson et al. 2001, Kemp et al. 2005, Inglis et al. 2006, Heggie & Savage 2009, Colby et al. 2010). These impacts influence the population connectivity of the meta-community within an estuary, potentially leading to fragmented populations, or

change from local to regional scale connectivity (Thrush et al. 2008, Cowen & Sponaugle 2009, Crook et al. 2015). For example, for a given estuarine bivalve species, a single bed is a 'population', whereas the meta-population includes all beds (populations) that are connected (locally or at a regional scale). Removal of source populations from the meta-population via coastal development, land reclamation or habitat destruction, significantly affects the transfer of individuals, and may eventually lead to population fragmentation or decline (Figure 1-2). Prior to development these populations are connected, with a consistent supply of new recruits, becoming fragmented or isolated post-development, with self-seeding dominating.



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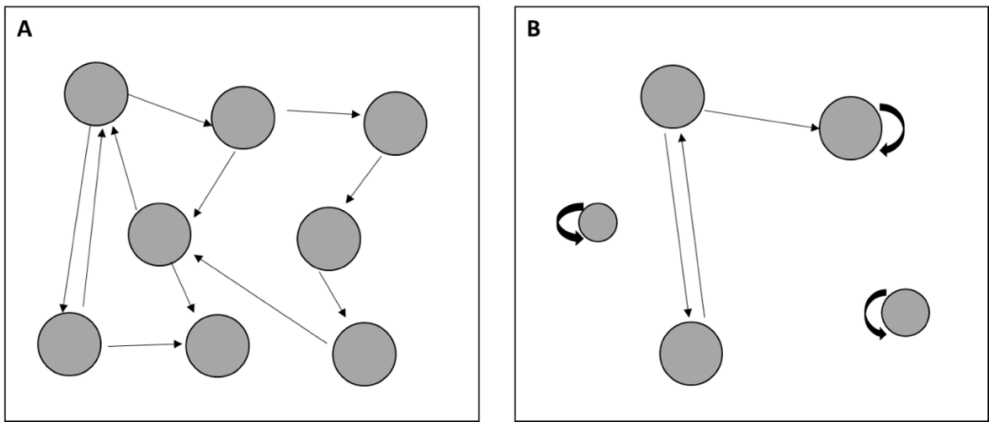

Figure 1-2: Potential impact of coastal development on population connectivity. A: Pre-development connectivity, transfer between populations within the meta-population are common, all populations are open. B: Post-development connectivity, loss of populations from the meta-population, self-seeding populations are increasingly common.

The scale at which connectivity occurs in estuaries varies, and the transfer of individuals between populations may occur regionally (inter-estuary connectivity) or locally (intra-estuary connectivity) (Cowen et al. 2006, Gawarkiewicz et al. 2007, Pineda et al. 2007, Thrush et al. 2008, Cowen & Spounagle 2009, Shanks 2009). Within a local scale of connectivity, the meta-population is contained within a single estuary, and is controlled by local factors such as within harbour retention during the dispersal phase, residual circulation and larval behaviour (Cowen et al. 2006; Jessopp & McAllen 2008; Levin 2006). Whereas, at the regional scale, recruitment occurs between estuaries and is dependent on larval transport to the outer coast, and back into an estuary (Levin 2006, Cowen and Sponaugle 2009, Shanks 2009). This life history is also common among some taxa, including species of crustacean (Mense & Wenner 1989). For purposes of gene flow and re-establishment of populations, long distance or inter-estuary connectivity can be significant (Underwood & Fairweather 1989, Cowen et al. 2007, Lowe & Allendorf 2010). However, regional scale dispersal is strongly influenced by coastal features such as fronts, gyres and coastal currents (Pineda et al. 2007, Pineda et al. 2010, Nickols et al. 2015), potentially introducing additional risk to individuals finding suitable habitat. For the purposes of population management and the implementation of conservation efforts, understanding local connectivity is of greater importance.

Population persistence requires there to be greater or equal new recruits (births and immigration) to a population than losses (mortality and emigration), and is influenced by population connectivity (Cowen & Sponaugle 2009). Inputs into a population are controlled by the production of recruits from a source population (externally sourced or self-seeding), mortality during the larval stage, and dispersal to the sink population (i.e. the transfer of these new recruits to the population). Larval mortality is high during the pelagic phase (potentially >90% for benthic marine invertebrates; Rumrill, 1990 as cited in Metaxas & Saunders, 2009), therefore, requiring high spawn counts from the source population. Dispersal in the marine environment is largely controlled by the interaction between organisms and tidal flow (Cowen & Sponaugle, 2009).

Estuarine populations were previously thought to be open, due to the length of the pelagic phase (hours to weeks), and relatively short flushing times in estuaries

(Levin, 2006, Cowen & Sponaugle, 2009, Shanks, 2009). From this conclusion, it would be expected that inter-estuary connectivity is high. However, there is increasing evidence that the local hydrodynamics and larval behaviour increase intra-estuary retention (Levin 2006, Jessopp & McAllen 2008, Metaxas & Saunders 2009, Shanks 2009).

Tidal transport in estuaries significantly influences the direction and distance of larval transport, and transfer between the source and sink populations is based on this dispersal pathway. Understanding the dispersal characteristics and the locations of source populations within an estuary is vital to ensure these conservation or management efforts are successful. However, quantifying dispersal pathways of benthic marine invertebrates is difficult, due to larval size and density, and there is often a lack of understanding of the hydrodynamic properties of many estuaries (Cowen & Sponaugle, 2009). To overcome this, a range of methods have been applied. These methods have included drifter release (e.g. Gawarkiewicz et al. 2007, Haase et al. 2012), quantifying genetic differences between populations (e.g. Becker et al. 2007, Hedgecock et al. 2007, Ross et al. 2012), and tag and release field monitoring (Jones et al. 2005, Almany et al. 2007). All methods have advantages and disadvantages; for example, drifter release provides only a snapshot of the conditions at the time of release, and does not predict dispersal during differing conditions. Genetic studies can show where transfer of individuals has occurred, however, the temporal scale of this connectivity often is not relevant to population management. Tag and release techniques are difficult due to the number of larvae that are required to be marked, handling effects, and the recapture of larvae following release (Levin, 1990, Thorrold et al. 2002). Results of these research methods can however provide calibration and validation data sets for the purpose of dispersal model development.

Direct tracking of larvae in the field is difficult, and due to advancement in modelling techniques and hardware, the use of hydrodynamic models to estimate population connectivity in marine organisms has increased recently (Levin, 2006; Metaxas & Saunders, 2009). Hydrodynamic models are often coupled with particle tracking modules to predict larvae dispersal, and to aid management decisions (e.g. Young et al. 1996, Lundquist et al. 2004, 2009, Haase et al. 2012, Bidegain et al. 2013, and Nicolle et al. 2013). For example, Lundquist et al. (2004) focused on

larvae release at four locations within the Okura estuary (North Island, New Zealand), and Lundquist et al. (2009) investigated dispersal of cockles within the Whangarei Harbour. The advantages of these coupled models include, the ability to understand current population dynamics, run scenarios based on environmental or anthropogenic change, and the ability to aid management.

1.2. Benthic marine invertebrates

Benthic marine invertebrate communities provide a number of ecosystem functions, including sediment stabilisation, roles in nutrient cycling, water column filtration and transfer of energy to higher trophic levels (Thrush et al. 2008, 2013). However, due to increasing pressures from anthropogenic changes, losses of benthic marine populations are common, influencing biodiversity and ecosystem resilience (Thrush et al. 2008, 2017). In estuarine communities, losses in biodiversity from disturbance have been shown to reduce ecosystem functions (Thrush et al. 2006, 2008). For example, the removal of bivalves from the sediment in Thrush et al. (2006) impacted on nitrogen cycling, with a reduction of ammonium efflux. Previous research has also identified a greater resilience to environmental stresses (such as nutrient or sediment loading) with increased macrofauna biodiversity (e.g. Thrush et al. 2006, 2017, Lohrer 2010).

Dispersal of many benthic invertebrates occurs during a pelagic larval stage that can last for hours to weeks (Cowen et al. 2006, Levin, 2006, Cowen & Sponaugle, 2009, Shanks, 2009; Figure 1-3). Following settlement, larvae metamorphose into juveniles, assuming the adult form and transition into the benthic habitat. The juvenile stage lasts from weeks to months, and recent research indicates that dispersal is possible during this period (Norkko et al. 2001, Hunt et al. 2009, Jennings & Hunt, 2009, Valanko et al. 2010; Pilditch et al. 2015). During the adult life stage many species are sessile (Bidegain et al. 2013), reliant on the early life stages for dispersal to occur. Therefore, previous dispersal and connectivity studies have focused on the transport and transfer of individuals during the early life stages.

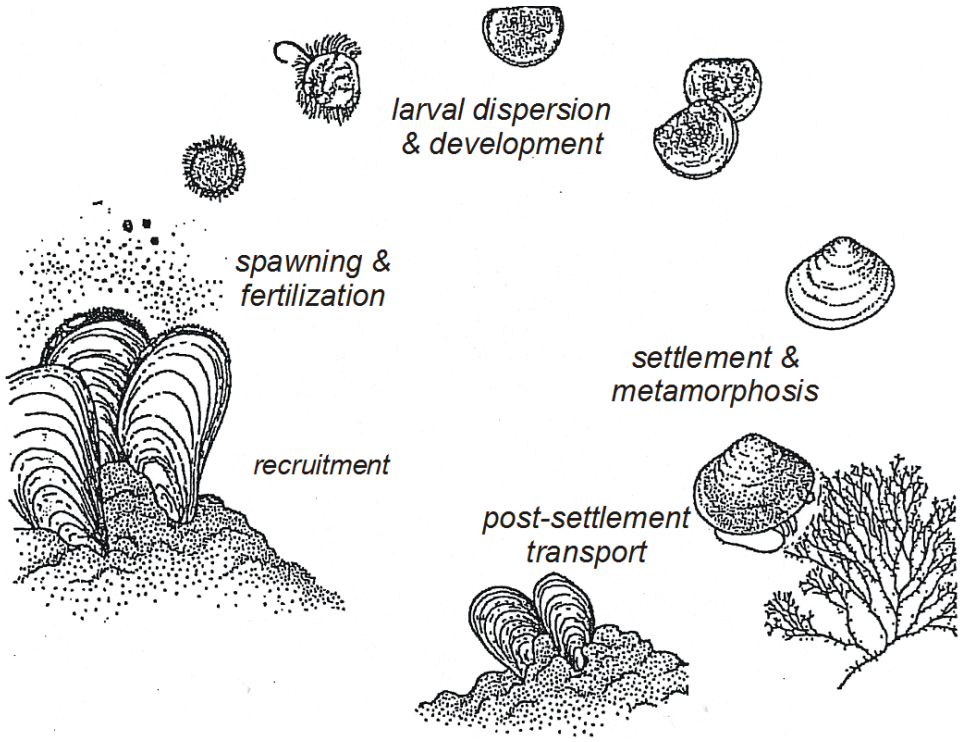

Figure 1-3: Life history stages of many benthic marine invertebrates. Modified from Wildish & Kristmanson (1997)

1.3. Increasing anthropogenic pressure on estuaries

Coastal development, land use change and intensification, climate change, and over harvesting have placed increasing pressure on marine ecosystems globally (Jackson et al. 2001, Kemp et al. 2005, Levin, 2006, Cowen & Sponaugle, 2009). Land reclamation and channel dredging have altered the tidal circulation and significantly impacted on community dynamics of many estuaries (e.g. Kenny & Rees, 1994, Colby et al. 2010). Land use change and the intensification of agriculture has altered nutrient cycles and increased sediment loading, with eutrophication, anoxia and hypoxia, and increased turbidity now common (Jackson et al. 2001, Kemp et al. 2005, Jones et al. 2011b). Excessive harvesting through poor fisheries management and lack of understanding of marine populations have led to the collapse of fisheries, local extinction of species, and ecosystem shifts (Jackson et al. 2001, Kemp et al. 2005).

Although New Zealand has a relatively short development history, estuaries are influenced by increasing anthropogenic pressures. Harbour and catchment development, channel dredging, increased shipping, and nutrient and sediment runoff from agriculture are now common (Inglis et al. 2006, Heggie & Savage,

2009). In many cases, these pressures have negatively affected benthic communities, through losses in habitat and increased fragmentation (e.g. Turner & Schwarz, 2006), changes to nutrient cycling and terrestrial sediment input (e.g. Thrush et al. 2004), and the occurrence of invasive species (e.g. Haywood, 1997). The ability of the benthic marine invertebrate communities to recover from these stresses is reliant on the supply of new recruits. Therefore, a better understanding of population connectivity in New Zealand estuaries is needed for effective management.

1.4. Thesis aims and organisation

My thesis aims to describe how the hydrodynamics in a large meso-tidal coastal lagoon, with complex morphology, influences intra-estuary transport and retention of benthic marine invertebrates. It is expected that further understanding of the local hydrodynamic conditions in estuaries will aid population management and conservation decisions. The main body of my thesis contains two research chapters: Chapter 2 describes the study location, and the numerical model development, calibration, and testing. Chapter 3 applies the developed model to assist in the interpretation of field data that describes spatial and temporal variations in benthic invertebrate larvae.

Chapter 2

Previous hydrodynamic modelling in Tauranga Harbour shows that water residence times vary due to residual tidal flows. However, the influence of these residual flows on larval dispersal have not been investigated. Therefore, the aim of this chapter was to develop and calibrate a hydrodynamic model with greater horizontal resolution than previously used and couple this to a larval tracking program. The model was developed and tested for sensitivity due to model parameter selection, and is described within this chapter.

Chapter 3

Previous hydrodynamic modelling in estuaries has highlighted the influence of local hydrodynamic conditions on larval transportation distances and intra-harbour retention. This chapter aimed to show how complex morphology affects tidal circulation, and the influence of this on larval dispersal and retention. I analysed a

data set from an earlier study, which collected, sorted and identified benthic invertebrate larvae from the surface and bottom water of the water column. Spatial and temporal variations in the larval community are described from this data set. With the addition of other water column characteristics, including temperature, conductivity, and tidal current speed and direction, transportation pathways were inferred. The numerical model that is described in Chapter 2 was applied to confirm the transport pathways and to identify retention regions in Tauranga Harbour that potentially provide a source of new recruits for benthic invertebrate populations.

Chapter 2. Hydrodynamic model

2.1. Introduction

Hydrodynamic models are often used for understanding processes in estuaries (e.g. population connectivity, tidal circulation, effects of dredging or harbour modifications; Lundquist et al. 2004, North et al. 2008, 2011, Spiers et al. 2009; Tay et al. 2013). The models applied range in scale and complexity, from small scale (e.g. Bartzke et al. 2016) to regional or global scale models (e.g. Matsumoto et al. 2000, Hasse et al. 2012). Therefore, several modelling packages options are available, and are selected based on the study requirements. 3DD (e.g. Lundquist et al. 2004), Delft-3D (e.g. Spiers et al. 2009), the Estuary, Lake and Coastal Model (ELCOM; e.g. Tay et al. 2013) and the Regional Ocean Modelling System (ROMS; e.g. North et al. 2008, 2011) have previously been applied to better understand estuarine scale processes. The purposes of these studies have varied and include investigations of dredging and morphological effects on coastal processes (e.g. Spiers et al. 2009), estimations of residual circulation and residence time of water in estuaries (e.g. Tay et al. 2013) and description of dispersal of larvae or oil (e.g. Lundquist et al. 2004, North et al. 2008, 2011). Delft-3D was selected for my study as it is an open source package, that is regularly updated and has a large user base. The model package allows for the creation of grids at finer scale than that of which ROMS is generally implemented (10s of meters compared to 100s of meters or larger grid cells). This finer scale was needed to resolve cross channel morphological changes and to give greater detail in the intertidal regions.

As it is understood that dispersal of benthic invertebrates predominantly occurs during the pelagic larval phase (Cowen & Sponaugle, 2009, Pineda et al. 2007, Pineda et al. 2010), coupled hydrodynamic-transport models focus on this stage (e.g. Hill, 1990, Lundquist et al. 2004, North et al. 2008, Roberts, 1997). The complexity of these models range from two-dimensional passive transport (e.g. Hill, 1990, Roberts, 1997) to those that include larval behaviours (e.g. Herbert et al. 2012, North et al. 2008, Broekhuizen et al. 2011). I selected the Lagrangian Transport (LTRANS; North et al. 2008, 2011) to simulate the transport of virtual larvae in this study. It was selected as it had been previously applied to the transport

of oyster larvae in Chesapeake Bay and allowed for future simulations, which include behaviour, to investigate larval dispersal and population connectivity.

2.1.1. Chapter aim and objectives

The aim of this chapter was to provide a calibrated hydrodynamic model with higher resolution bathymetry than previously applied for the southern basin of Tauranga Harbour, and couple this to a larval tracking model. This model was developed to be used for the interpretation of larval dispersal pathways, and to identify potential source and/or retention regions in Tauranga Harbour.

2.2. Study location

This study was carried out in Tauranga Harbour, New Zealand, a large (218 km^2) meso-tidal, barrier-enclosed lagoon (Figure 2-1). Tides in the harbour are semi-diurnal with a spring-neap range of 1.6 to 1.2 m. Harbour morphology is characterised by extensive areas of intertidal flats (approximately 66% of total area) and networks of subtidal channels. The harbour has two distinct drainage basins (northern and southern; Figure 2-1, panel B) which are separated by a large area of intertidal sandflat which restricts water exchange (Barnett, 1985; de Lange, 1988). This means the two basins can be considered as separate entities (Tay et al. 2012, 2013). My study focuses on the southern basin, a region with low fresh water input (~30 m^3s^{-1}; Park 2004), a large tidal volume (278 $x10^6$ m^3 at mean sea level) and is considered to be well mixed and flushed (water residence estimated at 2-8 d; Tay et al. 2013; Stewart et al. 2017). The southern basin is developed around the harbour entrance where channel dredging and land reclamation has occurred to accommodate shipping (Inglis et al. 2006). Tauranga Harbour was selected for this study as it is typical of many New Zealand estuaries (Hume et al. 2007), and meso-tidal coastal lagoons are common globally (e.g. Duffy et al. 1989; Riggs et al. 1995; Newton et al. 2014). This estuary type is characterised by low fresh water input, generally well flushed, and directly connected to the outer coast (Heath 1976).

2.2.1. Previous hydrodynamic modelling in Tauranga Harbour

There have been several numerical investigations of the hydrodynamics in the southern Tauranga Harbour. These studies have included description of the ebb-jet at the harbour entrance, which is influenced by dredging of shipping channels (Spiers et al. 2009); assessment of the sources and fate of sediment in the harbour

(Pritchard & Gorman, 2009); investigation of proposed coastal protection structures within the harbour (McKenzie, 2014); and estimation of water residence time and residual currents under differing wind and tidal conditions (Tay et al. 2013). However, intra-estuary population connectivity and larval dispersal were not previously investigated. To ensure that cross-channel changes in morphology were captured in this study, a new model with a finer resolution than previously used for the entire estuary was required.

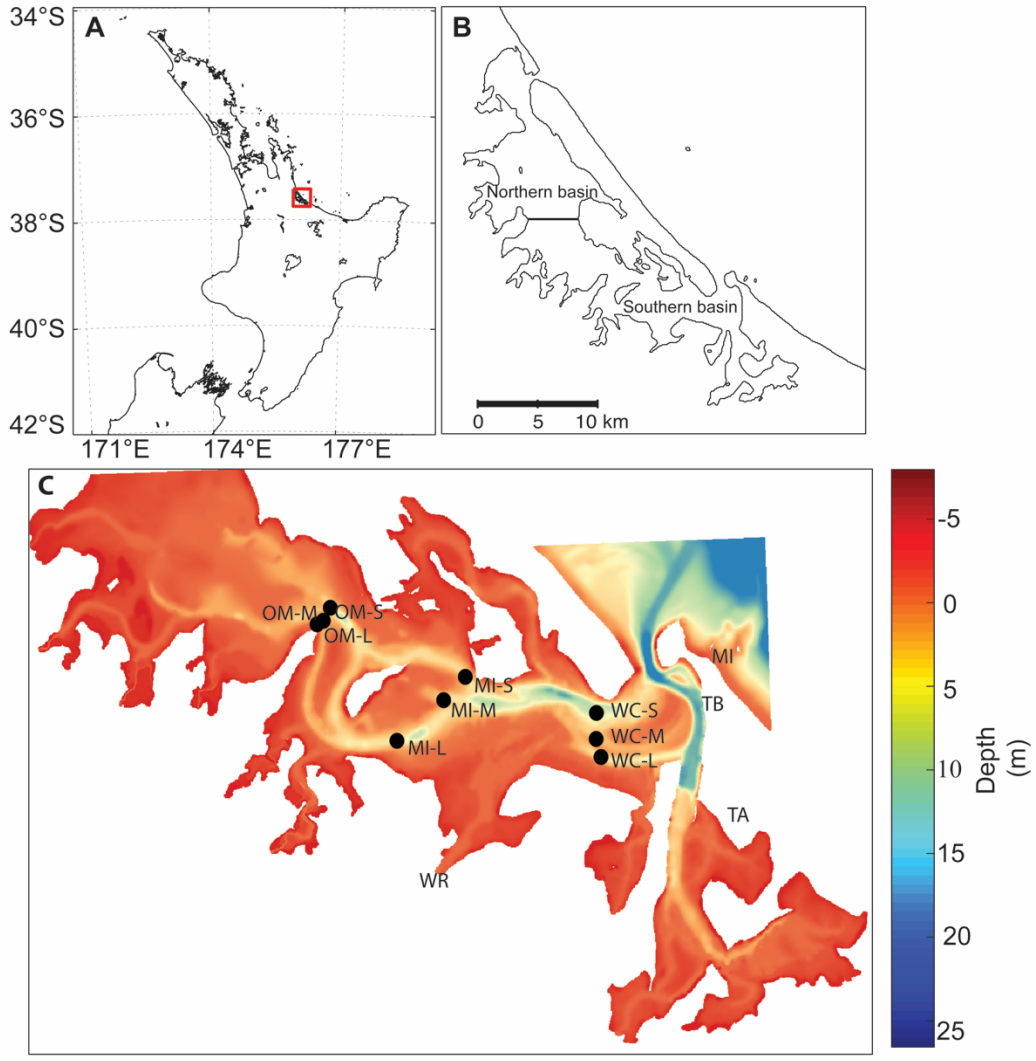

Figure 2-1: Location of Tauranga Harbour on the east coast of New Zealand (A & B) and model bathymetry of the southern basin (C). Field observation stations were aligned across three landward-seaward transects (OM, MI and WC; circle symbols; see text for explanations of transect abbreviations). Place names referred to in the text are also shown; Moturiki Island (MI), Tauranga Aerodrome (TA), Tug berth (TB) and Wairoa River (WR).

2.3. Methods

2.3.1. Field data used during model development and calibration

A six-day field deployment was carried out from 3rd to 11th February 1999 along three landward to seaward transects (3 sites per transect) across a lower harbour to upper harbour gradient (Figure 2-1). During this campaign surface and bottom water samples were taken approximately every 1.5-2 h for 48 h per site (Figure 2-1 & Table 2-1), which were filtered and larvae collected within these samples were identified to broad taxonomic level. Vertical profiles of temperature and conductivity collected with an Ocean Sensors 2000 CTD were also taken at the same time. On the days which larval sampling occurred for each transect (refer Table 2-1 for specific transect-position timing), an Interoceans S4 current meter was deployed at 1 m above the seabed, recording current speed and direction at a sampling rate of 1 min every 5 min at each of the transect positions. A water pressure sensor was deployed on the most landward S4 (i.e. OM-L, MI-L & WC-L; Figure 2-1), providing a water level time-series for each transect.

To aid modelling decisions, the collected field data was analysed for any evident trends in water column stratification or larval differences between the surface and bottom, diurnally. Differences between the surface and bottom waters were calculated for temperature, conductivity, and density. The cross transect larval samples were pooled with the proportional difference between the surface and bottom calculated ((surface – bottom)/(surface +bottom)) to see whether diurnal variation occurred. The taxa composition was also compared for diurnal variation at high and low tide.

Table 2-1: Details of the 1999 field measured hydrodynamic variables

Transect-Position	Location (NZTM)		Sampling period
	Easting	Northing	
OM-L	1869470.5	5831381.4	0300 h Feb 3 – 0635 h Feb 5
OM-M	1869661.6	5831470.7	0300 h Feb 3 – 0655 h Feb 5
OM-S	1869876.8	5831820.3	0300 h Feb 3 – 0640 h Feb 5
MI-L	1871722.9	5828118.1	0300 h Feb 6 – 0700 h Feb 8
MI-M	1873137.5	5829184.9	0300 h Feb 6 – 0700 h Feb 8
MI-S	1873797.5	5829800.2	0300 h Feb 6 – 0840 h Feb 8
WC-L	1877725	5827476.2	0300 h Feb 9 – 0745 h Feb 11
WC-M	1877599.6	5827973.6	0705 h Feb 9 – 0950 h Feb 11
WC-S	1877631.3	5828686.3	0300 h Feb 9 – 1025 h Feb 11

Abbreviations: OM: Omokoroa transect, MI: Motuhoa Island transect, WC: Western Channel transect; L: Landward position, M: Mid position, S: Seaward position. Refer Figure 2-1 for station locations

2.3.2. Hydrodynamic model development

Delft-FLOW (Deltares, 2011) allows the user to select from two- (depth averaged flow) and three-dimensional (vertical layered) hydrodynamic simulation. Tauranga Harbour is a vertically well-mixed estuary with little vertical stratification (Table 2-2). Therefore, a two-dimensional Delft-FLOW model (Deltares, 2011) was selected. All model creation was carried out with the tools provided by the Windows based Deltares GUI, with simulations carried out in parallel on the Linux platform.

2.3.2.1. Model grid

A rectangular model grid with a horizontal resolution of 20 m for the inner harbour was created for the southern basin of Tauranga Harbour using the Delft3D-RFGRID tool (Deltares, 2011; Figure 2-1 C). This resolution was selected to balance computation time, while attempting to resolve sub-estuary or cross-channel morphological differences and to incorporate greater detail across the inter-tidal areas.

2.3.2.2. Model bathymetry

The Delft-QUICKIN tool was used to calculate the model bathymetry, where depth data was sufficient, grid cell averaging was applied (intertidal and shipping channels), with triangular interpolation used in data sparse regions. A combination of LiDAR (1 m horizontal resolution; provided by Bay of Plenty Regional Council) in the intertidal areas, multibeam ecosounder (1 m horizontal resolution; provided by the Port of Tauranga) in sub-tidal channels (predominately in the port shipping channels) and digital LINZ (Land information New Zealand) chart data was used in bathymetry generation. These depth data were previously adjusted to chart vertical datum (Moturiki datum) and NZTM projection in Matlab by Martin Poot. The channels were checked and deepened or smoothed in required locations. Adjustments occurred near river mouths to stop river inflows from pooling, channels through intertidal areas, and the main channels around Motuhoa Island where high resolution subtidal depth data was not available. LiDAR collection over water surfaces adds uncertainty as these locations reflect and appear as a depth of 0 m compared to mapping datum. To avoid incorrect depths in the bathymetry, areas that appeared to have been collected from channels were not included from the LiDAR data during depth calculations. It is expected that due to the advances in water penetrating LiDAR, this limitation in future model implementation will be minimised (Smith et al. 2012). The bathymetry was adjusted to mean sea level, by adding 1.05 m to the depths.

2.3.2.3. Model input files and settings

There are several required and optional input details for Delft-FLOW (Deltares 2011). These files/parameters include the grid and bathymetry (as previously described), an enclosure file (automatically created by Delft-RFGRID during grid creation), boundary locations and conditions, wind forcing data, river locations and discharge, and run specific details (e.g. run dates, time step, and model output settings). The model boundaries were applied to the outer harbour edge of the model (North and East, Figure 2-1) using the M2, S2, N2, K2, K1, P1, Q1 and O1 constituents. These constituents were obtained by analysing the 1999 tidal record for Moturiki Island with T-Tide (Pawlowicz, Beardsley, & Lentz, 2002). Observed hourly averaged wind (2 m above the ground) data for the Tauranga Aerodrome (NZTM 1881944 5825723; Agent number 1614) was obtained from NIWA Cliflo

database (http://cliflo.niwa.co.nz; obtained 28/06/2013), and applied in all model simulations and during calibration. There are four gauged freshwater catchments, the Wairoa, Waimapu Waipapa and Kopurereroa Rivers, and six ungauged catchments that enter the southern Tauranga Harbour. The Wairoa River is the largest contributor to the harbour (mean discharge 17.6 m^3s^{-1}), and there is an estimated total surface water discharge of 30 m^3s^{-1} (Park, 2004). As surface water discharge is low compared to tidal flushing, an average discharge was applied to each of the catchments. Annual average discharge was applied to each of the gauged catchments, with the remaining catchments estimated based on catchment properties (size, land use and slope), with total discharge into the harbour calculated as equal to Park's (2004) estimate for the harbour. To ensure model stability a time step of 30 s was applied, and the first simulated day was not analysed allowing the model to reach equilibrium. Spatially variable Chezy's bed roughness was applied following calibration (refer to section 2.3.3), with all other parameters set to default.

2.3.3. Model calibration

During calibration, Delft-FLOW was simulated from 00:00 on 31 January 1999 until 23:59 on 28 February 1999, with the first 24 h of data not analysed, to ensure the model was at equilibrium. The hydrodynamic model was first calibrated for water level and the simulations checked to ensure that no ponding was occurring near river mouths. Water level observation data for the Port of Tauranga Tug Berth (NZTM 1880665 5829271; provided by the Port of Tauranga) for the month of February 1999, and water pressure sensor records were collected from each of the landward stations (i.e. OM-L, MI-L & WC-L; refer section 2.3.1 for a description of the field locations). A sensitivity analysis was undertaken by individually adjusting the uniform Chézy bed roughness, the model depth, and the eddy diffusivity coefficient. Prior to applying a spatially varying Chézy bed roughness, the best model fit for water level was achieved with default values for bed roughness and eddy diffusivity, with the bathymetry adjusted to mean sea level (+1.05 m from chart datum). Following water level calibration, current speed and direction (5 min averaged) was calibrated using the S4 (Interocean) current meter time series for each of the nine sites in the six-day field campaign. Initially a roughness map was created in Matlab based on the sediment regions in Hancock et al. (2009). This map allowed the bed roughness of the sub-tidal channels and

intertidal sand flat areas in regions of the harbour to be varied separately until a good model fit was achieved.

2.3.4. LTRANS coupling and testing

The Lagrangian transport model (LTRANS; North et al. 2008, 2011) was selected for estimating larval dispersal in this study. LTRANS was previously used to describe transport of oyster in Chesapeake Bay, and allows for future addition of pelagic larval behaviours. The model is forced by hydrodynamic simulation output, generally from the Regional Ocean Modelling System (ROMS) via offline coupling (i.e. the hydrodynamic simulation is run and then the transportation is calculated in a separate process). Transport distance and direction is calculated at a user defined time step for each larva that is released, and is within the modelled water column (i.e. has not left the model grid or settled (if settlement is enabled)). To minimise computer resource allocation, LTRANS obtains a sub-set of water column variables (temperature and salinity, unless constant (as applied in my study) and current velocity in the east and north directions (u & v, respectively), from a user defined number of grid nodes closest to the larvae at each hydrodynamic model time step. The average u and v velocities of the previous time step, current time step and next time step are calculated, and the larva is advected by the speed x time step in each direction (e.g. previous u = 1 m s^{-1} & v = 2 m s^{-1}; current u = 1.2 m s^{-1} & v = 1.5 m s^{-1}; next u = 1.3 m s^{-1} & v = 1.5 m s^{-1}; average u = 1.2 m s^{-1} & v = 1.7 m s^{-1}; time step = 10 s, the larvae is therefore moved 12 m east and 17 m north). There are several simulation methods that can be implemented in LTRANS, including passive transport, and simulations including behaviour specific to oyster. As there did not appear to be any trends that indicated a difference between the surface and bottom larval samples (see section 2.4.1, Figure 2-2), or strong diurnal behaviour (see section 2.4.1, Figure 2-3), passive transport was implemented in all LTRANS simulations.

LTRANS requires several input files, these include a grid mask (nodes that are included in the model), grid node locations (in latitude and longitude), model depths, and current speed (separate u & v variables; at each time step) for every grid node, which are generated by the hydrodynamic model. To my knowledge, LTRANS was not previously coupled to Delft-FLOW, and therefore, needed additional processing steps before use. The main differences between the output

files created by ROMS and the Delft-FLOW model applied are: the data format, I defined my grid using a New Zealand Transverse Mercator (NZTM) coordinate projection, and Delft-FLOW does not use a grid mask. Therefore, on conclusion of the hydrodynamic simulations, the output files were converted to the required formats in Matlab, the grid coordinates converted to New Zealand Geodetic datum 2000 (NZGD2000), and the grid mask was created.

LTRANS is an open-source model which requires compilation before use, which was achieved on the Linux platform using GFortran. As the software had not been compiled on the university computer system previously, and as the input files were converted before use, thorough testing of the model was needed. New output files were created by adding additional source code within the output steps of a model run. These files provided the location of every larva at each time step, and the east (u) and north (v) current velocities experienced. To ensure that LTRANS was obtaining current speed for the correct time step and grid cell, the output values were compared to the expected values in Matlab.

2.4. Results and discussion

2.4.1. Field data analysis

During the February 1999 field deployment there was no to little vertical stratification of the water column (Table 2-2), indicating that the harbour is vertically well mixed. Therefore, two-dimensional hydrodynamics were selected for modelling of tidal flows in the harbour. Proportional differences between the surface and bottom of the water column were highly variable, with no clear pattern across the transects for the pooled samples (Figure 2-2). There were weak diurnal trends for average proportional difference, which varied between transects. Average proportional slightly favoured surface transport in the day (0.05) and bottom transport at night (-0.05) for OM transect. This trend was reversed for MI transects (0.02 and 0.1 for day and night transport respectively). On average, the proportional difference for the WC transect slightly favoured bottom water transport (-0.1 and 0.01for day and night samples respectively). Larval composition varied spatially and temporally, with the greatest larval totals at the OM transect (Figure 2-3). Polychaete larvae generally dominated the OM transect during high and low tides, and the MI transect at low tide. Whereas, barnacle larvae was

dominant for WC, and at MI during high tide. Although there were no clear trends between the surface and bottom samples for the taxa observed, it is not possible to comment on the specific species, which may strongly vary.

Table 2-2: Mean difference (Δ) between the surface and bottom of the water column for temperature, salinity and density, measured during the February 1999 field campaign refer Figure 2-1 for locations. Values in brackets indicate observed ranges.

Transect-Position	Δ Temperature (°C)	Δ Salinity	Δ Density (kg m^{-3})
OM-L	0.061 (0.008 – 0.228)	0.060 (0.019 – 0.109)	0.06 (0.02 – 0.12)
OM-M	0.084 (0.002 – 0.524)	0.110 (0.036 – 0.442)	0.09 (0.02 – 0.49)
OM-S	0.080 (0.002 – 0.255)	0.270 (0.078 – 1.032)	0.23 (0.06 – 0.85)
MI-L	0.087 (0.027 – 0.184)	0.168 (0.052 – 0.444)	0.13 (0.02 – 0.31)
MI-M	0.057 (0.002 – 0.173)	0.157 (0.010 – 0.693)	0.13 (0.01 – 0.57)
MI-S	0.028 (0.003 – 0.073)	0.078 (0.006 – 0.222)	0.06 (0 – 0.19)
WC-L	0.238 (0.009 – 0.840)	0.242 (0.013 – 0.948)	0.24 (0.01 – 0.85)
WC-M	0.054 (0.002 – 0.184)	0.097 (0.006 – 0.312)	0.09 (0.01 – 0.21)
WC-S	0.064 (0.004 – 0.356)	0.098 (0.039 – 0.264)	0.08 (0.03 – 0.3)

Abbreviations: OM: Omokoroa transect, MI: Motuhoa Island transect, WC: Western Channel transect; L: Landward position, M: Mid position, S: Seaward position.

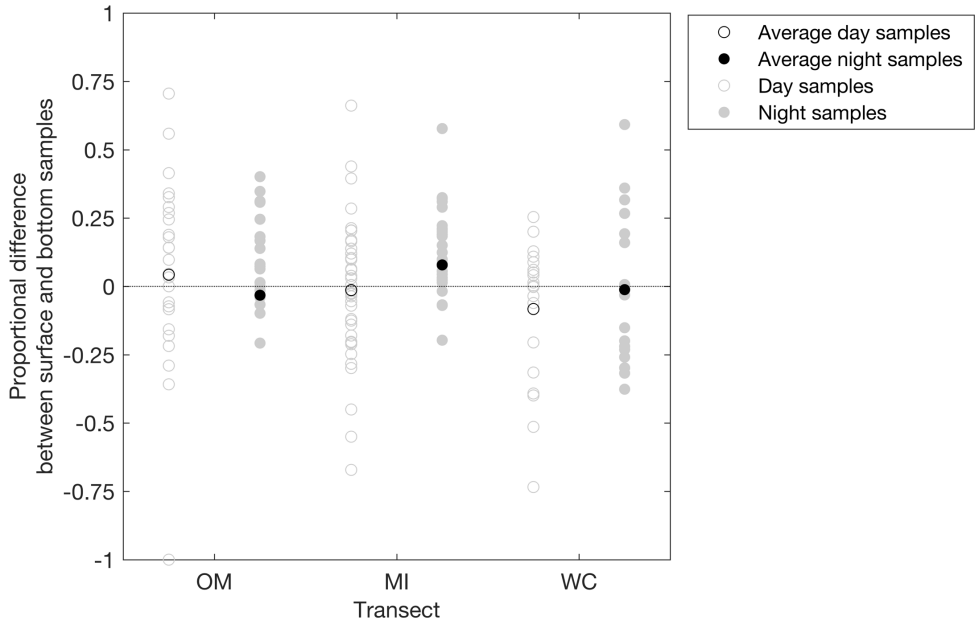

Figure 2-2: Proportional difference in total larval abundance between surface and bottom water samples (pooled across landward to seaward transects) for day (open circles) - and night-time (shaded circles) samples. Differences were calculated as (surface – bottom)/(surface +bottom) so negative values indicate great abundances near the seabed and positive values near the surface. The average values are indicated in solid circles. See Figure 2-1 for transect positions.

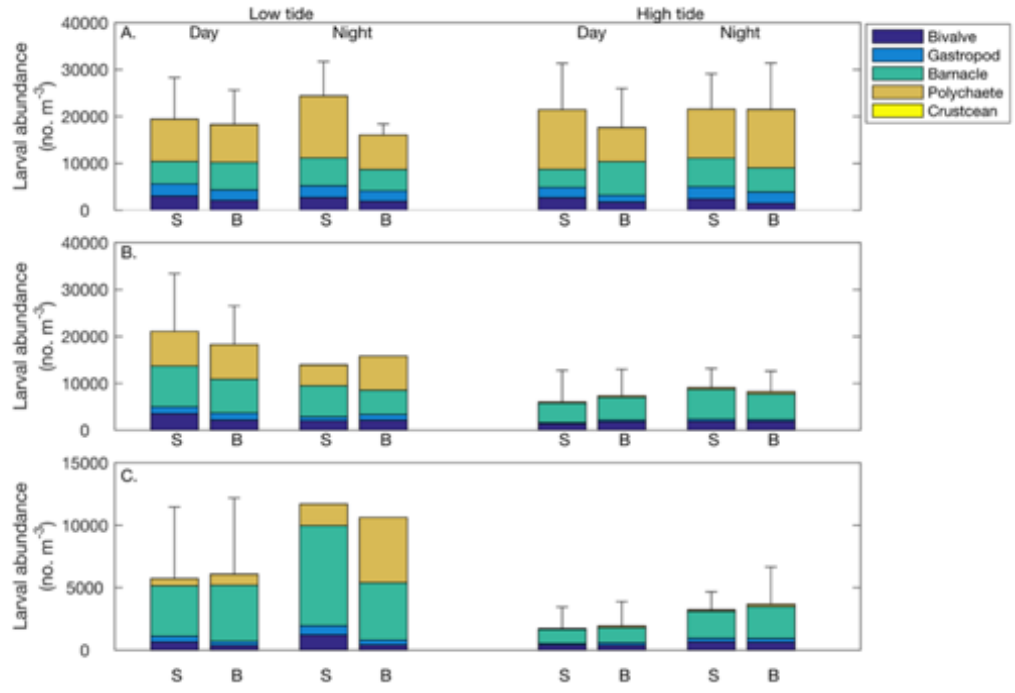

Figure 2-3: : Diurnal variations in mean larval abundance and taxa composition (pooled across transects) in surface (S) and bottom (B) samples at low (± 1.5 hours; LT) and high (± 1.5 hours; HT) tides for (A) OM (B) MI and (C) WC transects. Error bars indicate one standard deviation (n=2-12) and note the change in y axis scale between plots. See Figure 2-1 for transect-position locations.

2.4.2. Hydrodynamic model calibration

A good to excellent model fit was achieved for water level at all locations (Table 2-3, Figure 2-4 & Figure 2-5; error statistics are not given for Moturiki Island as this site was used as a visual check for boundary forcing). Good model fits for current speed were also achieved for all landward and mid transect locations (Table 2-4, Figure 2-6, Figure 2-7 & Figure 2-8) except for the landward position of the Omokoroa transect (OM-L) during flood tides. During flood tide at OM-L it appears that the dominant circulation bypasses the position of the S4 current meter, potentially due to morphological controls that were not resolved within the hydrodynamic model. During ebb tides, the model over-predicts current speed for the seaward sites. However, the S4 current meter was in the deeper channel of these locations, recording the lower water column and compared to depth averaged flows from Delft-FLOW. It is possible that the model fit in deeper channels would be improved if three-dimensional hydrodynamics were calculated due to boundary effects. Further field investigation, which measures current speed and direction at multiple heights would confirm these boundary effects in the channels, and provide further calibration data.

Table 2-3: Water level, amplitude and phase calibration results. Refer Figure 2-1 for locations.

Station	MAE (m)	RMSE (m)	M2 amp error (m)	M2 phase error (°)	S2 amp error (m)	S2 phase error (°)	K1 amp error (m)	K2 phase error (°)
OM-L	0.03	0.04	0.03	-0.80	-	-	0.01	6.06
MI-L	0.03	0.03	0.03	0.45	-	-	-0.00	5.46
WC-L	0.03	0.03	0.02	-0.07	-	-	-0.01	6.53
Tug Berth	0.06	0.07	-0.02	-0.55	0.00	13.36	0.00	11.21

Notes: MAE is mean absolute error; RMSE is root mean square. Abbreviations: OM: Omokoroa transect, MI: Motuhoa Island transect, WC: Western Channel transect; L: Landward position, M: Mid position, S: Seaward position.

Table 2-4: Current speed and direction calibration results. Refer Figure 2-1 for locations.

Station	Total			Flood		Ebb	
	Speed		Direction	Speed		Speed	
	($m\ s^{-1}$)		(°)	($m\ s^{-1}$)		($m\ s^{-1}$)	
	MAE	RMSE	MAE	MAE	RMSE	MAE	RMSE
OM-L	0.22	0.28	58.30	0.33	0.37	0.11	0.12
OM-M	0.10	0.11	28.97	0.08	0.09	0.12	0.13
OM-S	0.17	0.19	20.80	0.11	0.13	0.22	0.23
MI-L	0.07	0.07	28.14	0.06	0.08	0.05	0.07
MI-M	0.05	0.06	34.03	0.05	0.07	0.04	0.04
MI-S	0.10	0.13	29.08	0.06	0.08	0.15	0.16
WC-L	0.05	0.06	28.02	0.06	0.07	0.04	0.05
WC-M	0.04	0.05	20.80	0.04	0.05	0.04	0.05
WC-S	0.08	0.10	26.53	0.04	0.05	0.13	0.14

Abbreviations: OM: Omokoroa transect, MI: Motuhoa Island transect, WC: Western Channel transect; L: Landward position, M: Mid position, S: Seaward position.

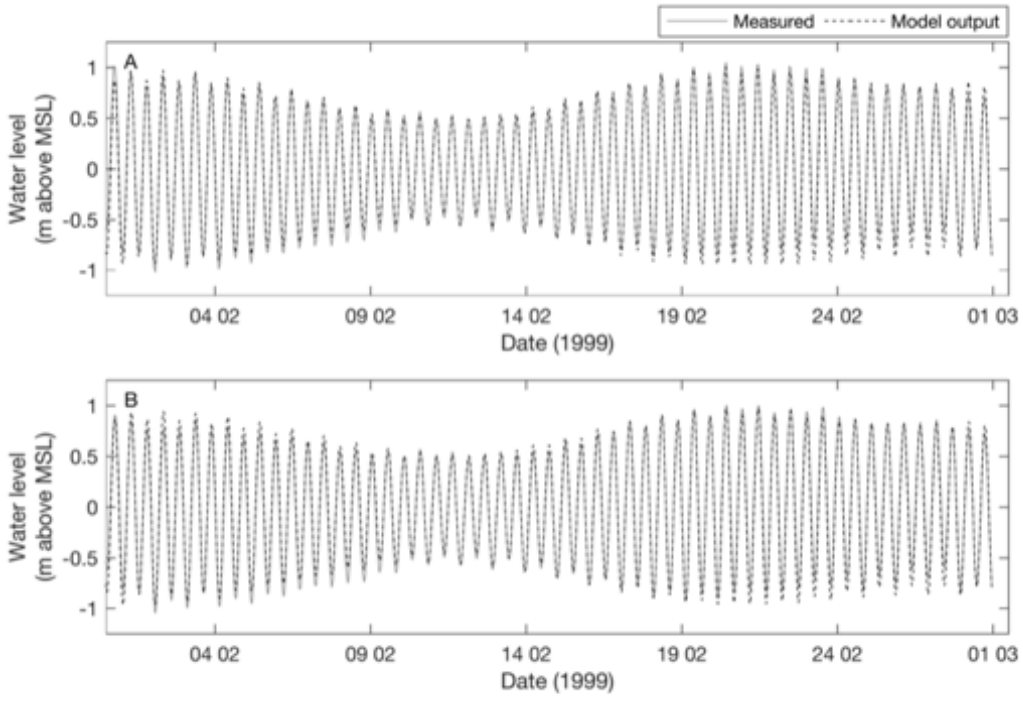

Figure 2-4: Water level model calibration (01-28 February 1999) for (A) Moturiki Island and (B) Port of Tauranga Tug Berth. Refer Figure 2-1 for locations.

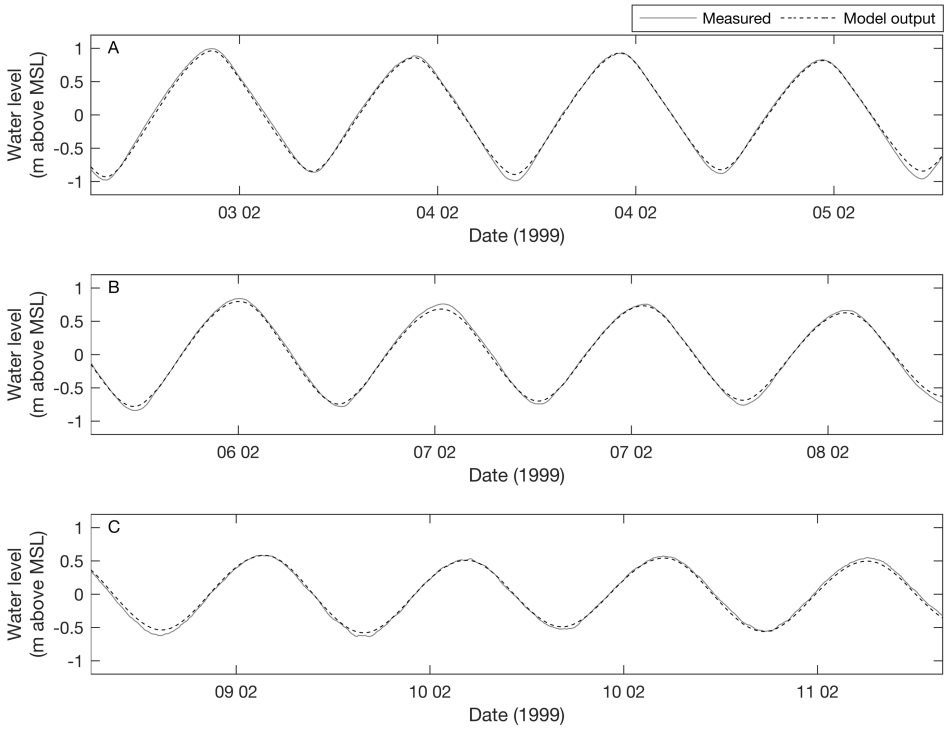

Figure 2-5: Water level model calibration for the landward positions of (A) Omokoroa (OM-L; 03-05 February 1999), (B) Motuhoa Island (MI-L; 06-08 February 1999) and (C)Western Channel (WC-L; 09-11 February 1999). Refer Figure 2-1 for locations.

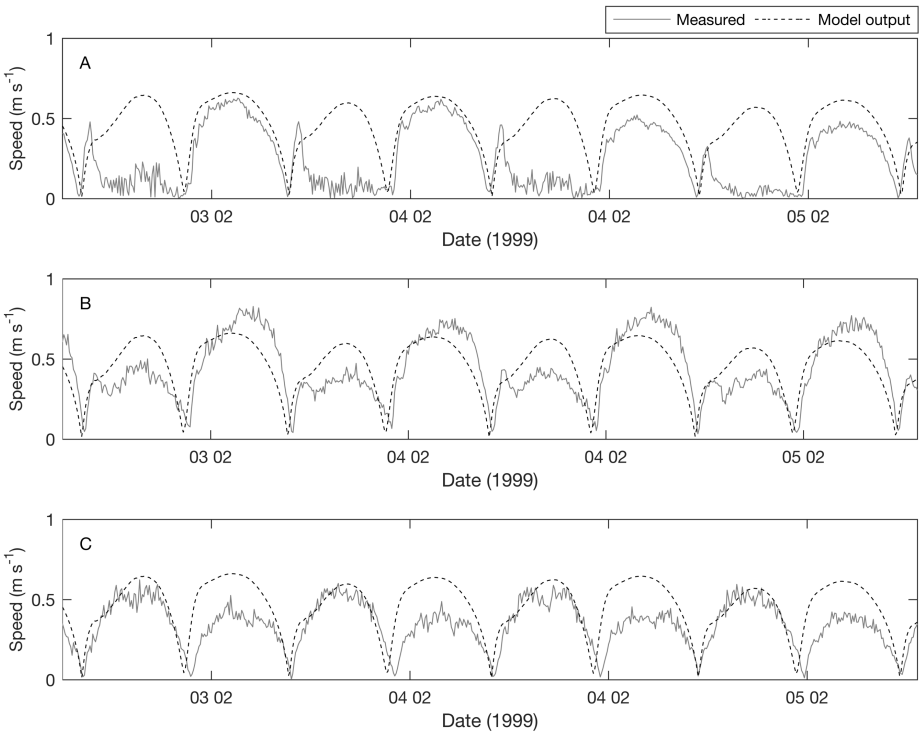

Figure 2-6: Current speed model calibration (03-05 February 1999) for Omokoroa transect (A) Landward (OM-L), (B) Mid transect (OM-M) and (C) Seaward (OM-S) positions. Refer Figure 2-1 for locations.

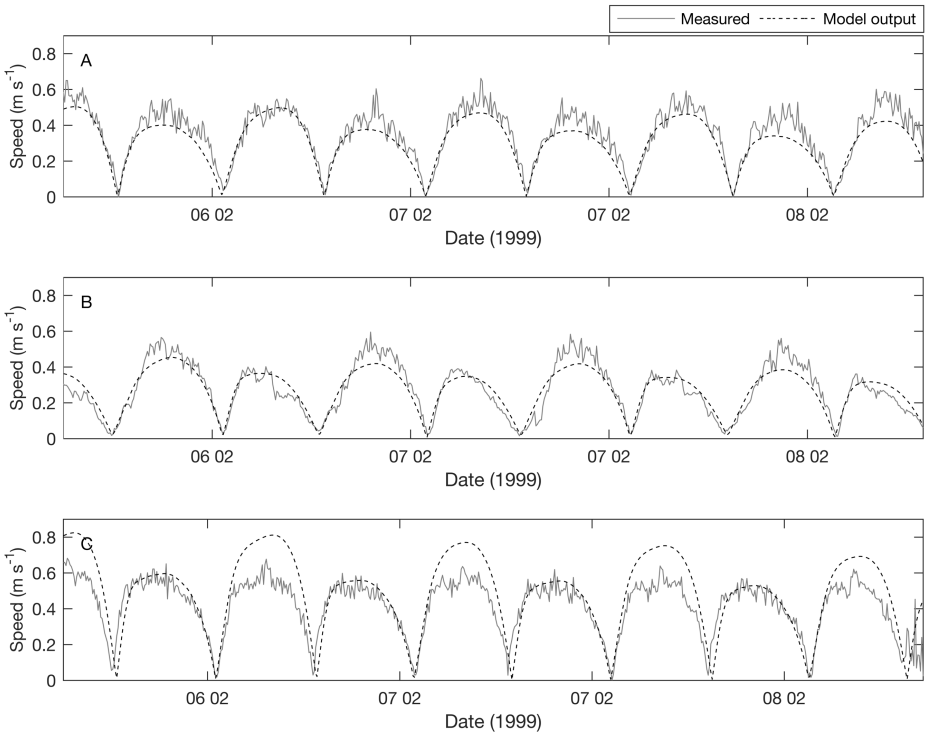

Figure 2-7: Current speed model calibration (06-08 February 1999) for Motuhoa Island transect (A) Landward (MI-L), (B) Mid transect (MI-M) and (C) Seaward (MI-S) positions. Refer Figure 2-1 for locations.

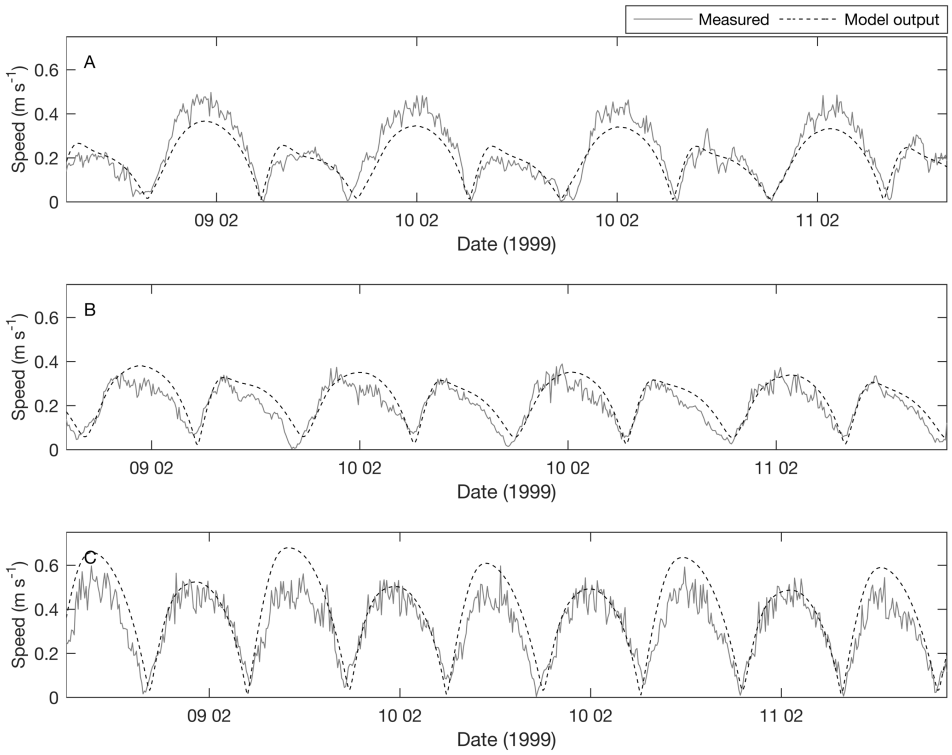

Figure 2-8: Current speed model calibration (09-11 February 1999) for Western Channel transect (A) Landward (WC-L), (B) Mid transect (WC-M) and (C) Seaward (WC-S) positions. Refer Figure 2-1 for locations.

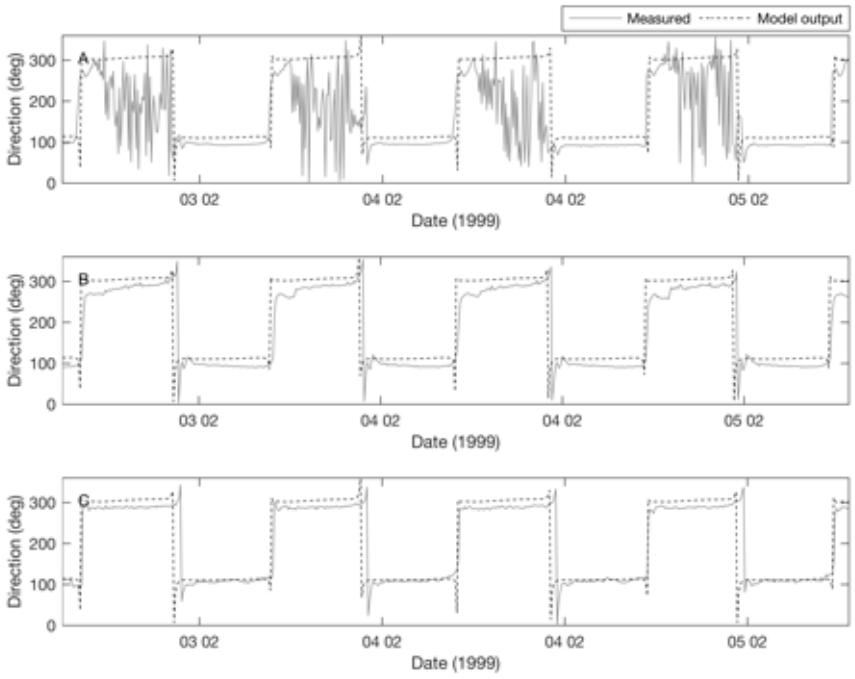

Figure 2-9: Current direction model calibration (03-05 February 1999) for Omokoroa transect (A) Landward (OM-L), (B) Mid transect (OM-M) and (C) Seaward (OM-S) positions. Refer Figure 2-1 for locations.

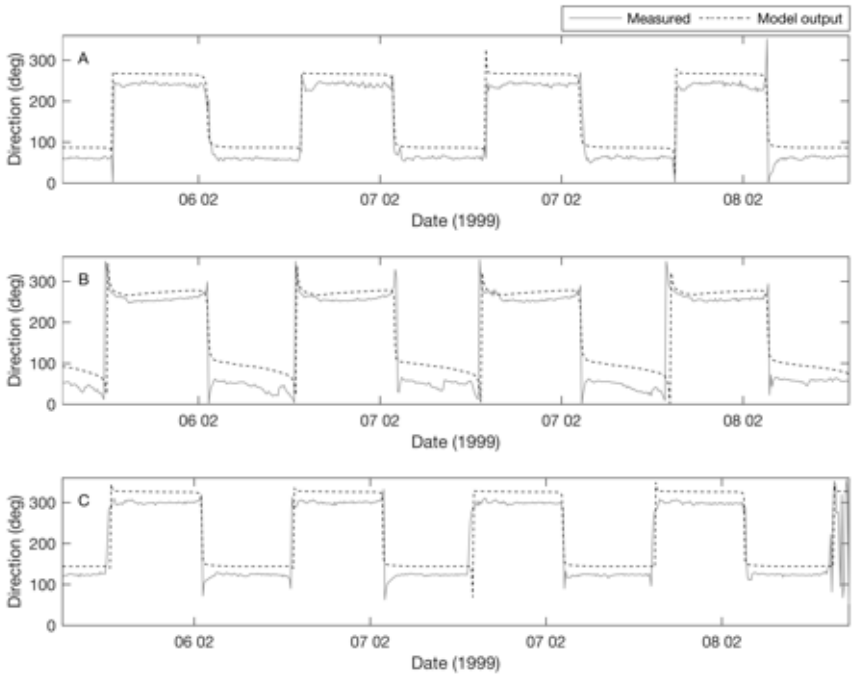

Figure 2-10: Current direction model calibration (06-08 February 1999) for Motuhoa Island transect (A) Landward (MI-L), (B) Mid transect (MI-M) and (C) Seaward (MI-S) positions. Refer Figure 2-1 for locations.

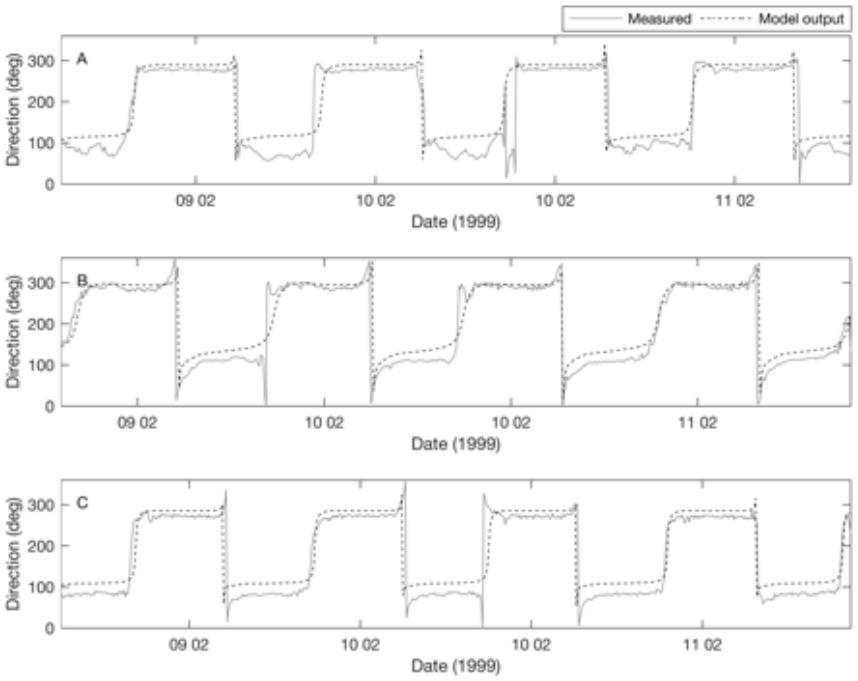

Figure 2-11: Current direction model calibration (09-11 February 1999) for Western Channel transect (A) Landward (WC-L), (B) Mid transect (WC-M) and (C) Seaward (WC-S) positions. Refer Figure 2-1 for locations.

2.4.3. Delft-FLOW-LTRANS coupling

Compilation of LTRANS, and the coupling of the model to the hydrodynamic model outputs from Delft-FLOW were successful. During the testing phase (Figure 2-12) of the model it was identified that LTRANS simulations were strongly influenced by the number of grid nodes the model obtained current speed data from at each hydrodynamic time step. If too few cells were selected, as a larva approached the outer edges of the subset of data, the distance a larva travelled was affected (i.e. the dips in the east velocity, see Figure 2-12 panel A, between time step 4000 – 5000). However, if the number of grid nodes was too large, the model crashed if the larval position was close to the edge of the bathymetry grid. Therefore, I used a buffer of 75 grid nodes (1.5 km) around each particle, to balance these effects. It was also evident that the time-step of the larval transport strongly influenced the model, where if the time step was too large, larvae would travel a distance greater than 1 grid cell width, causing the model to crash, too short and computation time was increased, thus I selected a time step of 1 s for all transport simulations.

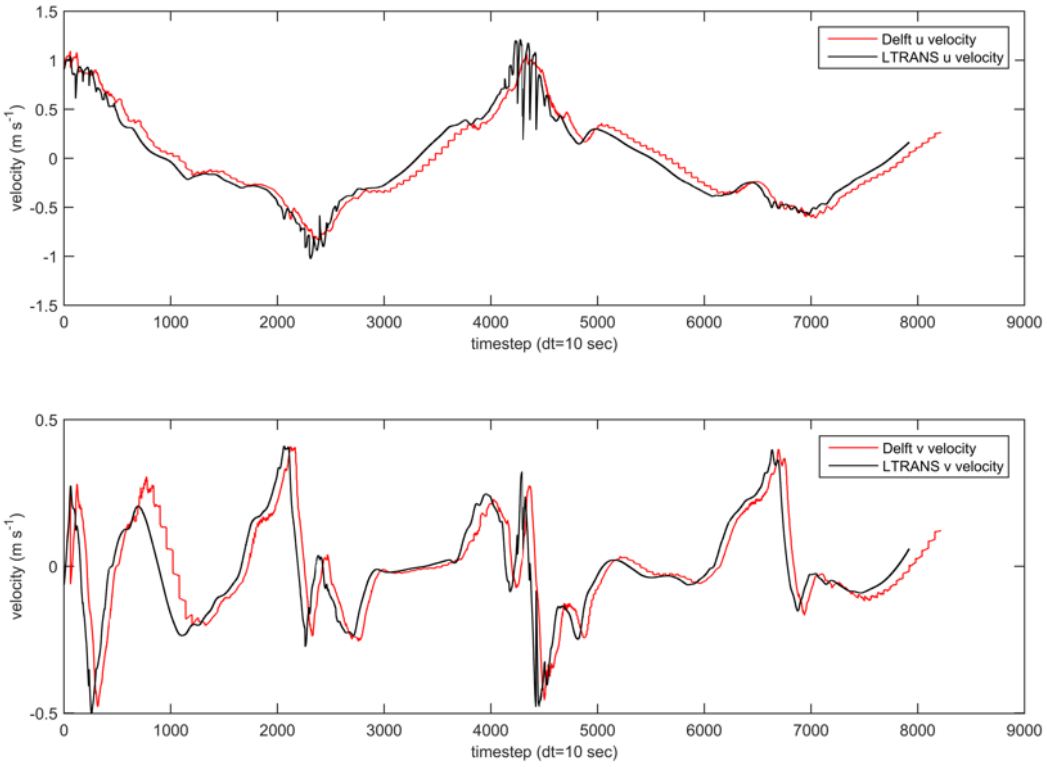

Figure 2-12: Expected current velocity from the hydrodynamic model output a larva should experience compared to the distance of dispersal in the (A) east direction (u) and north direction (v).

2.5. Chapter summary

A 20 meter horizontal resolution hydrodynamic model was developed and calibrated using field collected data. This model was coupled to a larval tracking program and release locations selected from differing regions of the southern Tauranga Harbour. The coupled hydrodynamic-transport model was tested, and sensitivity of model parameters identified.

Chapter 3. Transport and retention of benthic marine invertebrates in a large semi-enclosed meso-tidal estuary

3.1. Introduction

Understanding the supply dynamics of larvae into and out of marine populations is essential for the success of population management efforts (Botsford et al. 2008, Roughan et al. 2011, Siegel et al. 2003). Populations within an estuary can be referred to as meta-populations (or meta-communities) in which recruits can either be sourced within the estuary, sourced from another estuary by dispersal, or are exported from the system (Cowen & Sponaugle, 2009, Hanski, 1998, Nickols et al. 2015, Roughgarden & Iwasa, 1986). For many marine benthic invertebrates, dispersal is limited to the pelagic larval stage (Cowen & Sponaugle, 2009, Pineda et al. 2007, Pineda et al. 2010) which varies between species on the order of hours to weeks/months (Cowen & Sponaugle, 2009, Levin, 2006, Shanks, 2009). During this stage, due to the poor horizontal swimming capabilities of larvae, hydrodynamic induced transportation is critical to population supply dynamics (Young, 1995).

Benthic marine populations have previously been considered to be open, due to the length of the pelagic larval stage (Caley et al. 1996, Cowen et al. 2006). However, more recent research has shown that residual circulation patterns and/or larval behaviour can cause a dramatic reduction in the dispersal of larvae in coastal systems. For example, using a coupled hydrodynamic and particle tracking model Lundquist et al. (2004) found that most larvae travelled short distances, and settled within their release habitats. Similarly, Nickols et al. (2015) found that by including a coastal boundary layer within their simulations along the Californian coast, there was an increase of up to three orders of magnitude in self-retention compared to simulations that excluded this. These studies highlight that local hydrodynamic patterns within the coastal environment and larval behaviour can strongly influence dispersal and retention within, or export from an estuary (Cowen et al. 2006, Jessopp & McAllen, 2008, Levin, 2006).

The first stage of understanding population connectivity of benthic marine invertebrates is to have a detailed understanding of the tidal hydrodynamics and thus the transport pathways of pelagic larvae (Cowen & Sponaugle, 2009, Levin,

2006, Shanks, 2009). Hydrodynamic models have been used to predict dispersal because in situ tracking is difficult due to the small size and volume of benthic marine larvae (Cowen & Sponaugle, 2009, Levin, 2006, Shanks, 2009). These models have ranged in complexity from passive transport models (e.g. Hill, 1990, Roberts, 1997) to those that include larval behaviour, such as horizontal swimming, diurnal migration or salinity driven vertical migration (e.g. Herbert et al. 2012, North et al. 2008, Broekhuizen et al. 2011). These studies have successfully provided transportation and dispersal estimates of a range of benthic invertebrate species in the coastal environment. For instance, North et al. (2008) applied a coupled ROMS and LTRANS, with the addition of vertical swimming behaviour to transport model to simulate the dispersal of oyster larvae in Chesapeake Bay, in their study most simulated larvae did not return to the release reef, indicating open populations. In Broekhuizen et al. (2011), vertical swimming behaviour was added to their simulations of *Ostrea chilensis* in Tasman Bay to successfully match observed larval distributions.

Although these models provide a good overview of larval dispersal, the results are site specific, small-scale processes that influence the large-scale circulation are poorly represented and, in general, are not field validated. Field based studies of population connectivity have included genetic studies (e.g. Becker et al. 2007, Hedgecock et al. 2007, Ross et al. 2012), drifter releases (e.g. Gawarkiewicz et al. 2007, Haase et al. 2012), and surface plankton net tows (e.g. Bas et al. 2009). These field methods provide an overview of the population dynamics at a given time, however often are not further analysed to understand long term transport pathways. I have attempted to improve on these methodologies by combining field observations of benthic larval community composition and hydrodynamic measurements to predict larval transport pathways in a meso-tidal coastal lagoon, and confirmed these with numerical model simulations.

Shallow meso-tidal coastal lagoons are a common estuary type globally (e.g. Duffy et al. 1989, Riggs et al. 1995, Newton et al. 2014) and are also common in New Zealand (Hume et al. 2007). These lagoons are characterised by low freshwater input, direct connection to the coast and in general, are highly mixed and thought to be well-flushed (Heath 1976). However, intra-estuary morphological features including sand banks, islands, intertidal flats and the occurrence of ebb and flood

tidal channels complicate circulation patterns. Differences in tidal dominance is largely controlled by the relative proportion of sandflat area compared to tidal channels of an estuary, in which estuaries with extensive sand flats compared to channel depth and width are generally ebb dominant (Dronkers, 1986, Stive & Wang, 2003, Hunt et al. 2015). Sand banks, particularly when uncovered, and islands lead to flow diversion and/or flow partitioning, controlling circulation patterns. In areas where the bathymetry varies rapidly, circulation instabilities may develop and also influence tidal transport (Huppert & Bryan, 1976, Largier, 1993). Although the effects of morphologically induced flow instabilities and fronts on benthic larval dispersal have been examined in open coastal settings (e.g. McCullock & Shanks, 2003, Shanks et al. 2003a, Shanks et al. 2003b), to my knowledge, there are no similar studies in coastal lagoons.

In this study, I use spatially and temporally resolved observations of benthic invertebrate larval community composition and numerical simulations to answer the following question: how does channel morphology influence larval transport and retention in a large meso-tidal estuary? Larval transportation was assessed using a calibrated 2D hydrodynamic model that was coupled with a larval tracking module to aid the interpretation of the field observations. Retention was investigated using the model to determine the likelihood that different areas within the estuary act as source regions for benthic invertebrate larvae.

3.2. Methods

3.2.1. Study site

This study was carried out in Tauranga Harbour, New Zealand, a large (218 km^2) meso-tidal, barrier-enclosed lagoon (Figure 3-1). Tides in the harbour are semi-diurnal with a spring-neap range of 1.6 to 1.2 m. Harbour morphology is characterised by extensive areas of intertidal flats (approximately 66% of total area) and networks of subtidal channels. The harbour has two distinct drainage basins (northern and southern) which are separated by a large area of high intertidal sandflat which restricts water exchange (Barnett, 1985, de Lange, 1988). This means the two basins can be considered as separate entities (Tay et al. 2012, 2013). my study focuses on the southern basin, a region with low fresh water input (~30 m^3s^{-1}; Park, 2004), a large tidal volume (278 x 10^6 m^3 at mean sea level) and is

considered to be well mixed and flushed (water residence estimated at 2-8 d; Tay et al. 2013; Stewart et al. 2017). The southern basin is developed around the harbour entrance where channel dredging and land reclamation has occurred to accommodate shipping (Inglis et al. 2006).

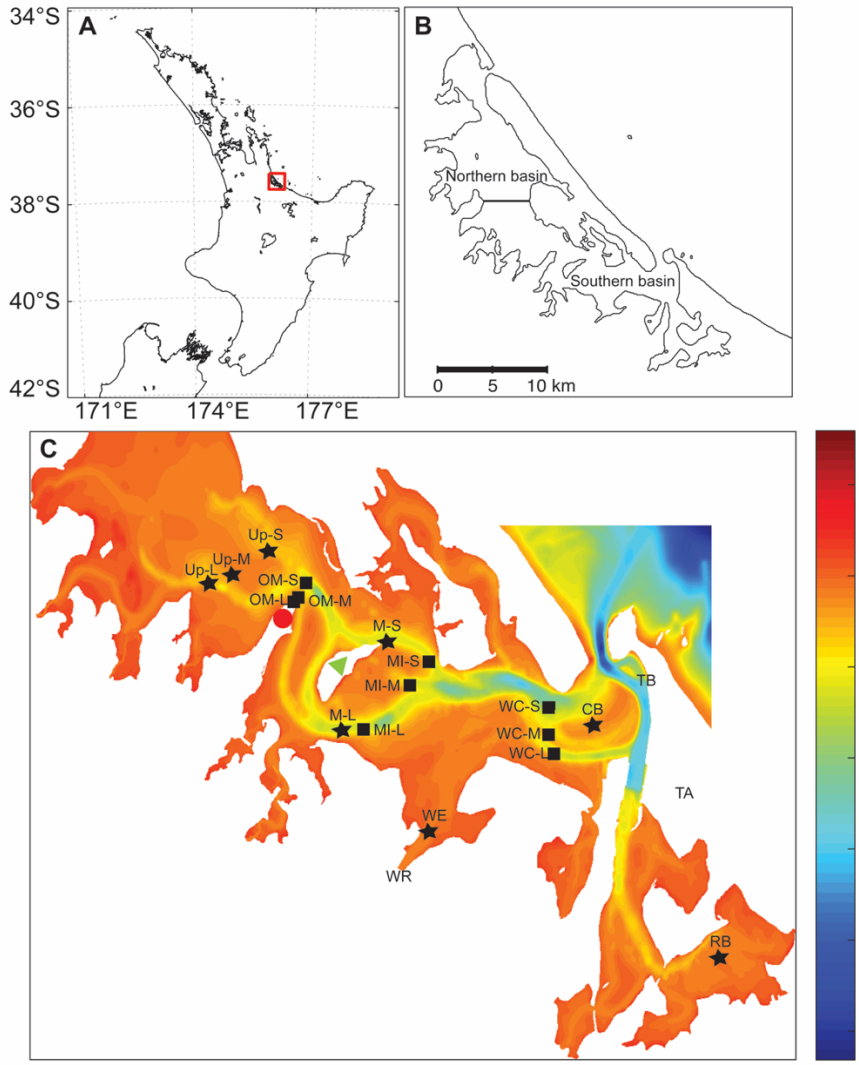

Figure 3-1: Location of Tauranga Harbour on the east coast of New Zealand (A & B) and model bathymetry of the southern basin (C). Field observation stations were aligned across three landward-seaward transects (OM, MI and WC; squares symbols), release locations (stars) for modelled larval transport (see text for explanations of symbol abbreviations). Place names referred to in the text are also shown; Omokoroa Point (red circle), Motuhoa Island (green triangle), Tauranga Aerodrome (TA), Tug berth (TB) and Wairoa River (WR).

3.2.2. Field observations

A six-day field campaign occurred in mid-summer from Feb 3-11 1999, sampling three landward to seaward transects from the upper (OM) to lower (WC) southern

basin (Figure 3-1). Across each transect, three sampling stations (landward (L), mid (M) and seaward (S)) were selected in sub-tidal channels to sample potentially different larval transport pathways. Each transect was occupied sequentially for 48 h starting with OM and ending with WC (Table 3-1). While sampling each transect, an Interocean S4 current meter was deployed 1 m above the bed at each station (logging interval 1 min every 5 min) to assist in model calibration. The S4 deployed at the most landward station was also fitted with a pressure sensor. Each station was sampled for benthic macrofauna larvae (see below) approximately every 1.5-2 h and at the same time a vertical profile of temperature and conductivity obtained (Ocean Sensors 2000 CTD). Equipment failure on the OM and WC transects meant 6 and 4 h of sampling, respectively were lost.

Larval samples were collected with a Lowara Domo 10 submersible pump located within 1 m of the surface and seabed. The pump was operated for 5 min (total volume sampled = 2.42 m^3) at each depth (1 m from water surface and seabed) and the water filtered through a submersed 75 μm mesh plankton net. The net was rinsed and the cod end contents preserved in formalin (approx. 4% final concentration) and stained with Rose bengal. In the laboratory, samples were diluted to 200 ml, mixed then split in half and one randomly selected for analysis. Samples were stirred in a figure-8 pattern to mix and a subsample removed with a wide mouthed pipette before being transferred to a gridded Perspex counting tray for identification and enumeration beneath a dissecting microscope. Benthic macrofauna larvae were identified to broad taxonomic units (bivalve, gastropod, crustacean, barnacle (naupili and cyprid), polychaete and echinoderm), and because abundance varied between groups and stations, the volume and number of replicate subsamples varied accordingly. Initially, three 1 ml subsamples were analysed. For rare taxa (< 10 $sample^{-1}$), a further 2 counts were taken from an increased subsample volume of 3 ml, and the remaining sample sorted if these further counts were still < 10 $sample^{-1}$ (Kimmerer et al. 1985). Because the water column was well mixed (see results) and preliminary analysis indicated no differences in benthic larval abundance between the surface and bottom samples (see section 2.4.1), I pooled data and report depth average abundance (no. m^{-3}). Multidimensional scaling analysis (MDS) was used to visualise spatial and temporal changes in larval community composition and was carried out in PRIMER7 (Clarke & Gorley, 2006).

Table 3-1: Details of the February 1999 field campaign to sample benthic invertebrate larvae in the southern Tauranga harbour basin. The number of larval samples represent a combined surface and bottom sample.

Transect-Position	Location		Sampling period	Mean depth	No. of larval samples
	Latitude	Longitude		(m)	
OM-L	37° 37' 30.760	176° 03' 12.191	0400 h Feb 3 – 0850 h Feb 5	2.03	16
OM-M	37° 37' 27.663	176° 03' 19.856	0400 h Feb 3 – 1225 h Feb 5	3.15	16
OM-S	37° 37' 16.110	176° 03' 28.160	0400 h Feb 3 – 1235 h Feb 5	6.13	16
MI-L	37° 39' 14.110	176° 04' 48.316	0400 h Feb 6 – 1025 h 8 Feb	6.16	24
MI-M	37° 38' 38.034	176° 05' 44.531	0400 h Feb 6 – 1040 h Feb 8	4.42	24
MI-S	37° 38' 17.389	176° 06' 10.592	0400 h Feb 6 – 1050 h Feb 8	5.66	24
WC-L	37° 39' 28.443	176° 08' 53.791	0400 h Feb 9 – 0850 h Feb 11	5.76	12
WC-M	37° 39' 12.463	176° 08' 48.001	0730 h Feb 9 – 12:45 Feb 11	4.39	12
WC-S	37° 38' 49.340	176° 08' 48.316	0400 h Feb 9 – 1250 h Feb 11	10.55	12

Abbreviations: OM: Omokoroa transect, MI: Motuhoa Island transect, WC: Western Channel transect; L: Landward position, M: Mid position, S: Seaward position.

3.2.3. Hydrodynamic model and calibration

Tay et al. (2013) estimated residence time of water for large regions of the southern basin using a 75 m resolution 3D hydrodynamic model. From Tay et al.'s (2013), study it is evident that there are regions of the harbour that are more retentive than others (2-8 d). To assist interpreting field data and to investigate how morphological features might influence larval transport pathways and retention in Tauranga Harbour, I developed a higher resolution rectangular model grid of 20 m (Figure 3-1) in Delft-FLOW (Deltares, 2011). The highest resolution data available was used in creation of the model grid i.e. LiDAR (1 m horizontal resolution) for the intertidal areas and multi-beam eco-sounder (1 m horizontal resolution) in the shipping channels (provided by Bay of Plenty Regional Council and the Port of Tauranga, respectively). Where no high-resolution bathymetry data was available, Land Information New Zealand (LINZ) chart data was used. All bathymetry depths were adjusted to mean sea level (1.05 m above chart datum).

As the water column was vertically well mixed during the study period (see section 3.3.1), Delft-FLOW was run in 2D (i.e. depth averaged flows) and flow was driven by tidal forcing, river input and wind. Tidal harmonic analysis of the 1999 tidal record at Moturiki Island (provided by the National Institute for Water and Atmospheric Research; NIWA) with T-Tide (Pawlowicz et al. 2002) was undertaken and astronomical tidal (M2, S2, N2, K2, K1, P1, Q1 and O1 constituents) forcing was applied to the outer boundary using the T-Tide output. Freshwater input from the 10 rivers and streams in the southern basin is low (~30 m^3s^{-1}; Park, 2004) and all were included in the model. The largest contributor of fresh water is the Wairoa River (mean flow = 17.6 m^3s^{-1}), with an additional three rivers continuously gauged; average discharge was estimated for the remaining inputs (based on catchment size and characteristics). Hourly averaged wind forcing was applied to the model from Tauranga Aerodrome for the modelling period (14 Jan – 28 Feb 1999), which represents typical summer wind patterns when benthic larval abundance in Tauranga Harbour is high (Booth, 1983, Giles, 2002).

The hydrodynamic model was calibrated using the S4 current and pressure sensor time series collected during the six-day field campaign. To ensure model stability, a model time step of 30 s was used. Spatially variable Chezy's roughness coefficient was applied and adjusted to achieve a good model fit for water level and flow

velocity. The root-mean squared error (RMSE) and mean absolute error (MAE) statistics were calculated between the measured and modelled flow characteristics. Good model fits for water level (<0.04 m for RMSE and MAE), and water velocity (<0.2 m s^{-1} for RMSE and MAE) were achieved for all locations apart from OM-I during flood periods. Further calibration details are provided in Chapter 2.

3.2.4. Larval transport model

The larval transport model, LTRANS (North et al. 2008, 2011) was coupled to the hydrodynamic output from Delft-FLOW. LTRANS was selected as it has been successfully used to model the transport of oyster larvae within the Chesapeake Bay and contains algorithms for future implementation of larval behaviour (North et al. 2008). Detailed larval behaviour for the benthic marine invertebrates common in Tauranga Harbour is not known, and because there was no detectable time-dependent vertical variation in larval abundance/composition in the shallow well mixed estuary, assumed neutrally buoyant, passive larval transport in all simulations. Neutrally buoyant particles were selected in attempt to capture a range of early life stage species. Because of this selection, my results are not representative of larger, heavier larvae or juveniles that would be negatively buoyant. Passive transport (e.g. Hill, 1990; Roberts, 1997) is often assumed, and justified because larvae have low swimming capability (e.g. Levin 2006; Cowen and Sponaugle 2009, Shanks, 2009). Although I did not include a mortality term, larvae that stranded for more than four days were considered to be lost from the system. I released 5,400 virtual larvae per simulation, with one larva released from the centre of nine grid cells surrounding a release location every 6 s (a total release rate of 9 larvae s^{-1}), and they were tracked with a 1 s time step.

To help interpret field observations from the OM and MI transects, I modelled the transport pathways of larvae released at mid-ebb tide from three up-harbour locations (Up-I, Up-M and Up-S; Figure 3-1). Larvae were released as passive tracers in the tracking model 18 d prior to the sampling of the OM transect (16 Jan 1999) and were tracked until 12 Feb 1999. A period of 28 d was implemented to ensure that any residual circulation patterns during a full lunar cycle were captured. Transport pathways were visualised from the position of larvae at mid-ebb tide 48 h and 28 d after release.

To determine whether areas within Tauranga Harbour have the potential to retain larvae, larvae were released under differing tidal conditions from eight locations in the southern basin (Figure 3-1). The release points cover a range of regions, including, the upper-, mid- and lower- harbour as well as sub-estuaries. Pelagic larval duration of benthic marine invertebrates varies between species and is generally in the order of days to weeks/months (Shanks, 2009). A pelagic duration of 16 d was selected, which is a period relevant to a number of soft sediment species (in particular clams; Stephenson & Chanley, 1979, Lundquist et al. 2009, Shanks, 2009), and is at the lower limit for pelagic duration for barnacle larvae (Barnes & Barnes, 1954, Shanks, 2009). Larval retention was estimated as the percentage of larvae remaining in the harbour after 16 d. Four simulations were carried out, spring high and low tide and neap high and low tide, to investigate the effect of both timing and location of release on retention.

3.3. Results

3.3.1. Field observations

Environmental variables measured during the field campaign indicate differences between sites (Table 3-2). Mean current speed ranged between 0.2 (WC-M) and 0.44 m s^{-1} (OM-M) with a maximum peak of 0.83 m s^{-1} at OM-M. The water column temperature was warmer with a lower salinity at the OM transect compared to the WC transect. Landward to seaward differences were also observed for the OM and MI transects, with warmer less saline water at the landward sites than that of the seaward sites. Vertical density stratification was small, indicating the water column was generally well mixed.

Table 3-2: Mean current speed, water column temperature (T), salinity (S) and density, and benthic larval counts measured during the February 1999 field campaign. Δ density is the difference in between the surface and bottom of the water column. Values in brackets indicate observed ranges expect for mean current speed where the peak value is given.

Transect-Position	Mean current speed (m^3s^{-1})	Mean T (°C)	Mean S	Mean Density (kg m^{-3})	Δ Density (kg m^{-3})	Mean larval abundance (no. m^{-3})
OM-L	0.25 (0.63)	23.0 (21.9 – 24.9)	33.1 (32.6 – 33.5)	1,022.5 (1,021.6 – 1,023)	0.06 (0.02 – 0.12)	18,121 (2,882 – -34,523)
OM-M	0.44 (0.83)	23.1 (21.9 – 24.8)	33.3 (32.8 – 33.7)	1,022.7 (1,021.7 – 1,023.2)	0.09 (0.02 – 0.49)	28,120 (18,244 – -37,650)
OM-S	0.34 (0.62)	22.8 (21.9 – 24.1)	33.7 (33.3 – 34.4)	1,023 (1,022.4 – 1,023.8)	0.23 (0.06 – 0.85)	19,495 (8,763 – -33,092)
MI-L	0.35 (0.66)	23.0 (22.4 – 23.7)	34.0 (33.6 – 34.6)	1,023.1 (1,022.8 – 1,023.8)	0.13 (0.02 – 0.31)	20,563 (1,451 – -45,919)
MI-M	0.27 (0.60)	22.7 (22.1 – 23.8)	34.3 (33.9 – 34.8)	1,023.5 (1,022.9 – 1,023.9)	0.13 (0.01 – 0.57)	12,909 (2,609 – -42,408)
MI-S	0.42 (0.68)	22.8 (22.2 – 23.5)	34.2 (33.3 – 34.8)	1023.4 (1,022.8 – 1,024)	0.06 (0 – 0.19)	11,677 (3,754 – -23,342)

Transect-Position	Mean current speed (m^3s^{-1})	Mean T (°C)	Mean S	Mean Density (kg m^{-3})	Δ Density (kg m^{-3})	Mean larval abundance (no. m^{-3})
WC-L	0.22 (0.50)	22.9 (21.6 – 24.1)	34.3 (33.6 – 34.8)	1,023.4 (1,022.6 – 1,023.9)	0.24 (0.01 – 0.85)	5,951 (2,227 – -20,110)
WC-M	0.20 (0.39)	22.7 (21.9 – 23.5)	34.5 (33.7 – 34.9)	1,023.6 (1,022.8 – 1,024)	0.09 (0.01 – 0.21)	3,890 (859 – -7,816)
WC-S	0.33 (0.60)	22.7 (22.1 – 23.8)	34.5 (33.6 – 34.9)	1,023.6 (1,022.7 – 1,024)	0.08 (0.03 – 0.3)	3,648 (970 – -14,755)

Abbreviations: OM: Omokoroa transect, MI: Motuhoa Island transect, WC: Western Channel transect; L: Landward position, M: Mid position, S: Seaward position.

Mean larval abundance varied spatially both from landward to seaward sites and between transects (Figure 3-2). Mean larval abundance was higher for the upper harbour (OM) transect (on average by >13,000 m^{-3}) than at the lower harbour (WC) transect. Larval abundance was also greater for the landward than the seaward site on the mid harbour (MI) and lower harbour transects. At high tide, larval counts for the upper harbour landward site (OM-L) were higher compared to the seaward site, however on average larval counts were greatest at the mid site of this transect (Table 3-2). Strong tidal variations were observed for all locations with eight of the nine locations having greater low tide than high tide counts. The only exception to this was the landward OM station (OM-L) where there were more larvae at low tide than high tide at the (Figure 3-2).

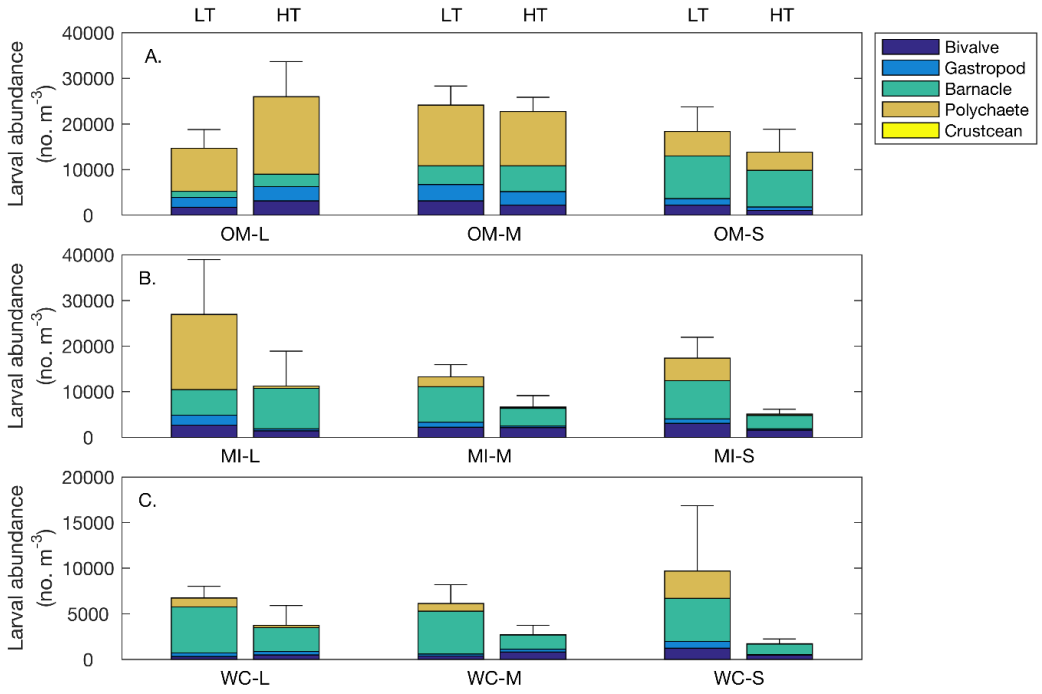

Figure 3-2: Mean larval abundance and taxa composition for low (± 1.5 hours; LT) and high (± 1.5 hours; HT) tides for (A) OM, (B) MI and (C) WC transects. Error bars indicate one standard deviation (n=6-12) and note the change in y axis scale between plots. See Figure 3-1for transect-position location.

Larval composition also varied spatially and temporally (Figure 3-2). The landward and mid OM sites were dominated by polychaetes (>50 %), followed by gastropods and bivalves, while barnacle larvae dominated the seaward site (>39 %). Barnacle larvae also dominated stations on the WC transect (>36 %) and the mid and seaward sites of MI (>42 %) at both high and low tides; however, clear tidal variations were evident for the landward site (MI-L). During low tide at the landward MI site, polychaete larvae were dominant (>48%) compared to high tide during which barnacles dominated (>41%).

Non-metric multi-dimensional scaling analysis (nMDS; Figure 3-3) was used to highlight differences in the community composition between sites and tidal stage. From this analysis, it is clear that the landward and mid OM sites cluster together with low variance, demonstrating a similar larval abundance and composition. At low tide, the landward and mid MI sites share similar community characteristics with OM-L and OM-M, potentially indicating the seaward transport of individuals from the upper harbour during ebb tides. The landward and mid MI sites also share similar community composition to that of the WC sites during the flood tide. At other times the MI-L and MI-M sites show a composition that is between the OM landward and mid, and WC sites, indicating a mixture of both communities. The seaward OM site shows similarities to the landward and mid OM sites, however there is also evidence of a different community composition more similar to the MI transect at high tide. The WC sites show the least similarity to the OM landward and mid sites and a high temporal variation. The spatial and temporal variation of community composition, particularly for the MI sites, is of particular interest, and provides evidence of asymmetry in larval transport pathways.

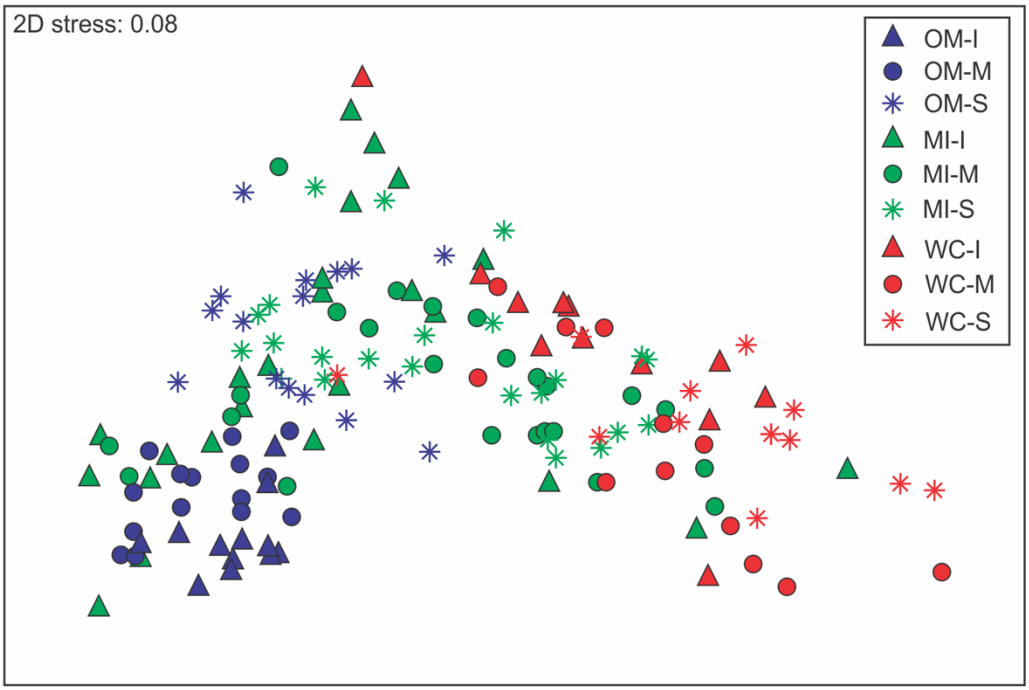

Figure 3-3: Non-metric MDS ordination (Bray-Curtis similarity) showing the spatial and temporal variation in benthic larval community composition for each transect-station. The closer the distance is between points, the more similarity the community composition. See Figure 3-1 for station locations.

3.3.2. Numerical model

3.3.2.1. Larval transport

To investigate the patterns in larval abundance/composition observed the OM transect stations during the field campaign, I released virtual larvae from above this transect, which were tracked for 28 d. Larvae were released in a landward to seaward transect (Up-L, Up-M & Up-S) at mid ebb tide. Two days after releasing the larvae, it was evident that larval transport was predominately within the landward channel around Motuhoa Island (Figure 3-4 A – C) for the three release locations. This modelled transport explains the similarities in low tide larval composition between the OM-L and OM-M and the MI-L and MI-M stations (i.e. Figure 3-2 & Figure 3-3). Water flow and larval transport is split around a sandbank between Motuhoa Island and Omokoroa Point (refer Figure 3-4). Larvae are transported within the landward channel of this sandbank close to Omokoroa Point when released at Up-L and the Motuhoa Island channel when released at Up-M (compare Figure 3-4 A & B). Both pathways are observed for benthic larvae released at Up-S. During the same length of time larvae are transported a shorter

distance if released at Up-L than that of both Up-M and Up-S, with the longest distance observed for Up-S released larvae. After 28 d (Figure 3-4 D – E), the dominant ebb tide transport pathway is still within the landward channel around Motuhoa Island. Over the modelled period, larvae were also transported to several sub-estuaries from the three release locations. There is also transport within the seaward channel, particularly for larvae released from Up-S. The observed transport pathways and position of larvae after 28 d show that the upper harbour may be a significant larval source or retention region; this is due to the extended transport pathway caused by Motuhoa Island and the asymmetric flows caused by the channel network in this region.

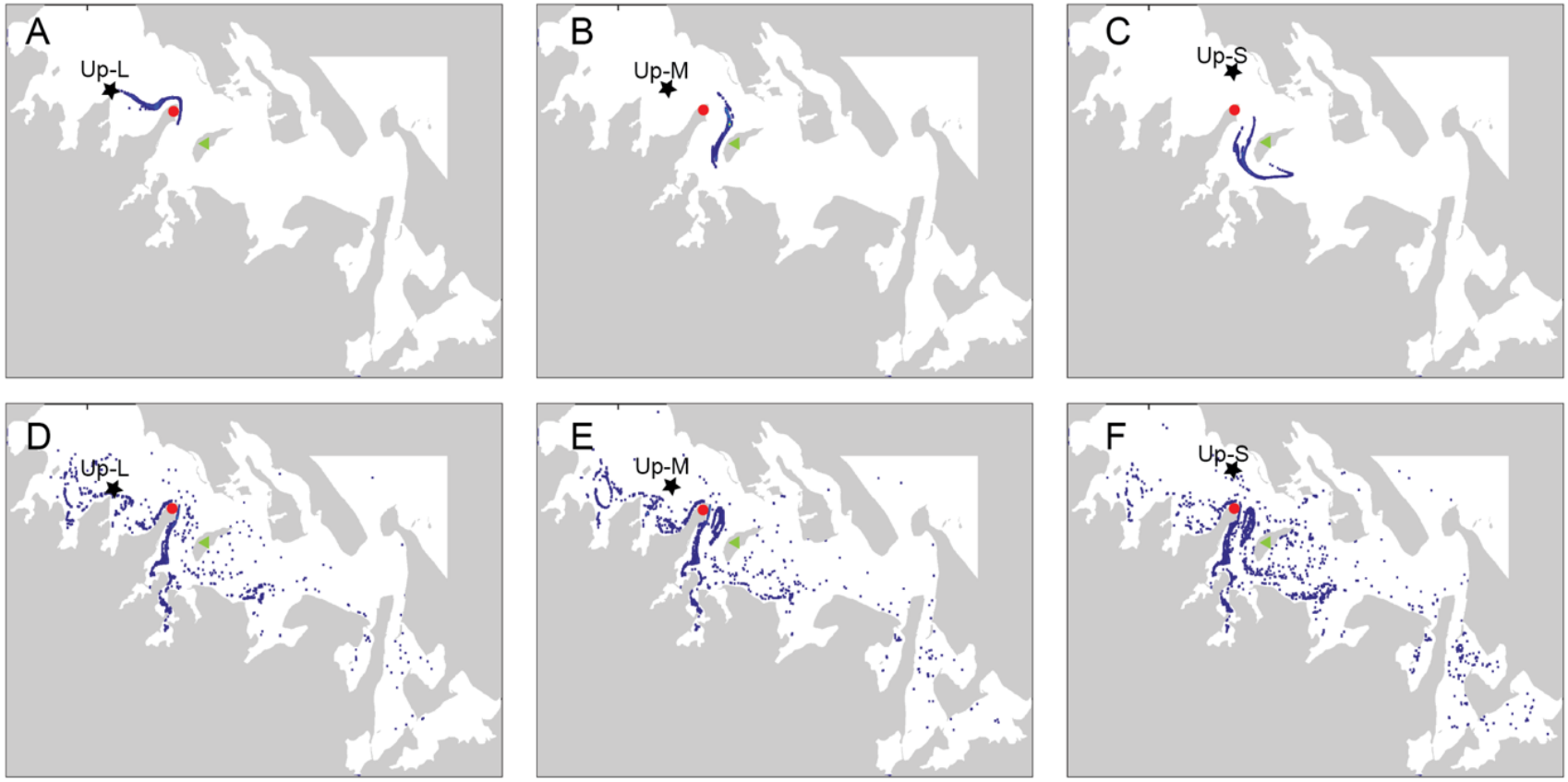

Figure 3-4: Modelled larval transport from three release locations (indicated by stars) in the upper southern basin of Tauranga Harbour 48 h (A-C) and 28 d (D-F) after release. The position of Omokoroa Point (circle) and Motuhoa Island (triangle) are also indicated.

3.3.2.2. Larval retention

Retention varied between the four release scenarios for all locations (Figure 3-5). Under all tidal conditions, the upper landward (UP) and mid harbour (M) sites retain more than 60% of larvae 16 d after release, with Up-M retaining a minimum of 79%. The seaward upper harbour release site showed a strong tidal dependence in which 100% of larvae released during a low neap tide were retained compared to a high neap tide release in which only 6% remain. For larvae released from the mid harbour landward (M-L) and seaward (M-S), retention was also highly variable (26 – 87% and 0 – 94% respectively). For these sites (mid harbour and upper-seaward), retention is highly dependent on the release timing (flood or ebb). Retention of larvae released near the harbour mouth (CB; centre bank) was always low (0 – 10%), with the highest retention estimated during a low neap tide release. Larvae released from the sub-estuary regions (WE & RB) show a tidally dependant retention: in a spring high and low tide release retention is low (4 – 10%) whereas during a neap tide release retention was increased to >60% and >80% for WE and RB respectively.

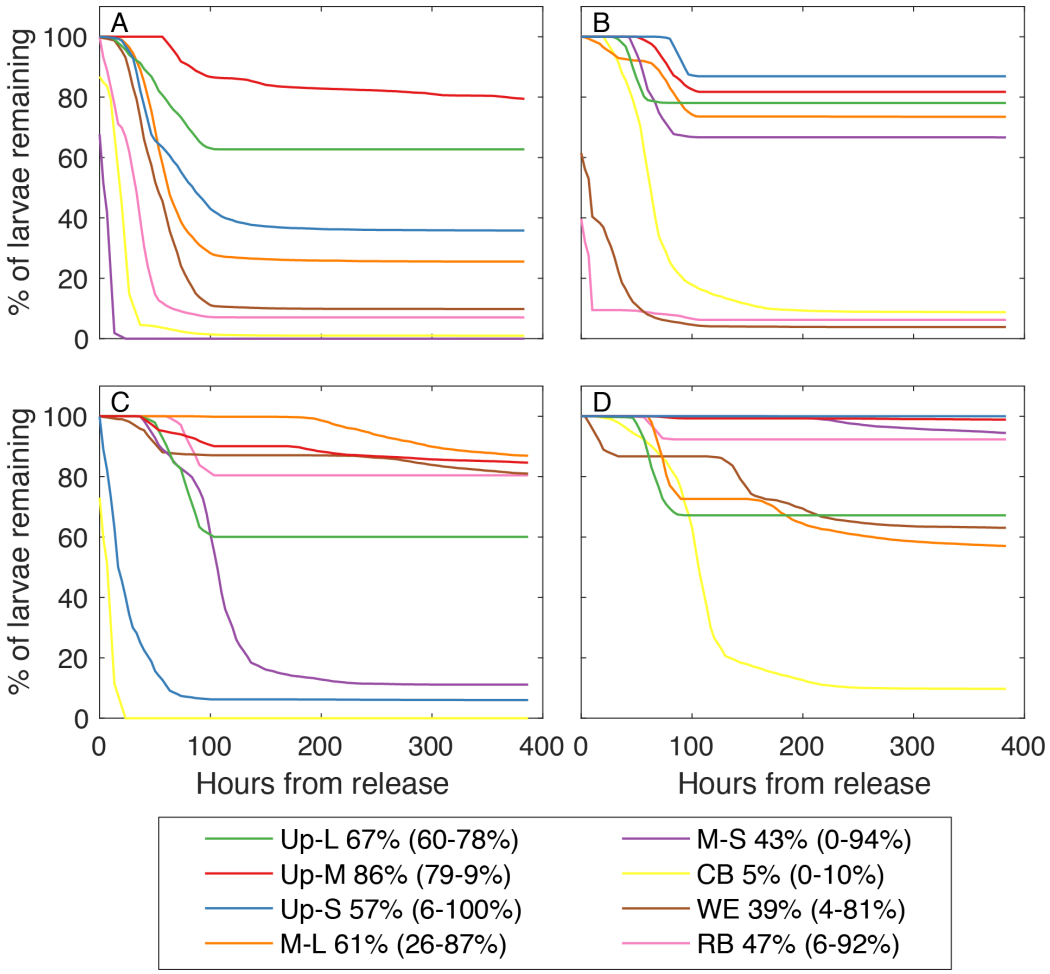

Figure 3-5: Modelled larval retention from eight spawning locations in the southern Tauranga basin (see Figure 1) during a 16 d period. Larvae were release under different tidal stages (A) spring-high, (B) spring-low, (C) neap-high and (D) neap-low tide and a five point moving average was applied to the data. The percentage of larvae retained in the harbour averaged across the different release scenarios along with the range (in brackets) is given in the figure legend.

3.4. Discussion

Environmental observations and larval sampling from the field campaign provide evidence of asymmetrical flow transportation. Cooler, more saline coastal water is transported within the seaward channel past the three seaward stations (WC-S, MI-S, and OM-S) during the flood tide. Oceanic larvae were carried within this body of water as evidenced from a larval composition dominated by barnacles and lower total abundance at high tide. In the vicinity of Omokoroa Point, some mixing of the oceanic and upper harbour water occurs (characterised by high total larval abundance and dominated by polychaetes). During the ebb tide flow path, a substantial portion of the upper harbour water enters the two subtidal channels around a sandbar between Omokoroa Point and Motuhoa Island (Fig 1 & 4). This transport pathway explains the observed variation in larval abundance and composition at the upper harbour (OM) and mid harbour (MI) landward locations. Larvae transported from the upper harbour through these channels result in increasing larval counts and alterations in community composition during ebb tide at MI-I. My numerical simulations for larvae released from upper harbour locations provide further evidence of these pathways. As the transport pathways are extended due to this asymmetrical flow, retention is increased within the harbour.

Tauranga Harbour has previously been described as a well-mixed and flushed estuary (e.g. Heath, 1976), with water residence times estimated by Tay et al. (2013) of up to 8 d. It would therefore be expected that larval retention is low; however, my results indicate that complex channel morphology influences retention within the estuary. In model simulations, larvae released up-harbour of regions influenced by morphologically controlled tidal circulation (i.e. Omokoroa Point, Motuhoa Island, an intertidal sand bank and the subsequent sub-tidal channels formed by these features; e.g. OM-I and OM-M release locations) had increased retention, and the level of retention was largely independent of release conditions (tidal stage). Retention from mid-harbour and sub-estuaries release locations was more varied and dependant on the magnitude of currents (e.g. neap vs spring tides) and the direction of initial transport (e.g. flood vs ebb tide). Larvae released in the mid harbour and sub-estuaries during neap tides experience lower current magnitudes, resulting in shorter initial transport distances and thus a higher retention. During flood tide releases, larvae are first transported towards the upper harbour, where

retention is higher due to morphological features. There are few numerical modelling studies that have shown the influence of complex morphology on simulated larval retention. For example, Herbert et al. (2012) showed that, in combination with behavioural cues, embayments in Poole Harbour increased retention of Manila clam. Additionally, previous studies have also indicated the contribution of larval release location and timing compared to distance of larval transport (e.g. Lundquist et al. 2004). Similarities exist in studies of retention in rivers and streams where channel formations such as pools and riffles can stagnant channel flow and create localised areas in which retention is increased (Bencala & Walters, 1983, Manson, 2000, Runkel et al. 1998). Although these freshwater systems are unidirectional, a similar process may occur within estuaries, where the position of sand bars and channels in areas such as between Motuhoa Island and Omokoroa (refer Figure 3-1 & Figure 3-4) generate areas of localised retention.

Numerical models are often used for predicting dispersal and retention of larvae in coastal systems (e.g. Herbert et al. 2012, Hill, 1990, North et al. 2008, Roberts, 1997). However, due to model limitations (e.g. grid cell resolution, position of calibration points, lack of biological samples), it is possible that processes on a scale of 10s to 100s of meters are neglected. Due to the difficulty of obtaining bathymetric measurements in shallow harbour regions, the resolution of collected data is often low and small scale morphologies omitted. However, with the constant improvements in water-penetrating LiDAR techniques, data will likely become easier to obtain. The significance of these morphological controls is particularly clear in the Omokoroa Point transect (OM-I, OM-M & OM-S), where morphological variability significantly influences the direction and distance of transport. Without the sampling resolution provided by the choice of site location (i.e. the transect of three sites spanning 100s of metres) and timing (i.e. the 1.5- 2 h for 48 h water column measurements), it would not be possible to resolve the significant variations in larval composition across this transect, which have effects on transport pathways. I have attempted to capture the smaller scale morphological variations with the use of a 20-metre resolution numerical modelling grid. Although a finer resolution may resolve these further, simulations would become computationally expensive.

There are many historical, large scale changes in Tauranga Harbour that may have influenced tidal circulation and altered dispersal pathways. These changes include harbour development and dredging, land reclamation, as well as catchment land-use changes that have altered sedimentation rates (de Lange, 1988, Inglis et al. 2006). Anthropogenic modification in estuaries is common globally, influencing large scale circulation. Land reclamation (e.g. Sheehy, 2009) and coastal dredging have been linked to a reduction in population connectivity due habitat loss (e.g. Sheehy, 2009, Colby et al. 2010). Changes to the circulation patterns will also influence the connectivity patterns by changing circulation patterns that advect planktonic larvae around the Harbour. Similarly, Colby et al. (2010) found that by dredging the channels of the Murray River mouth, a more ebb dominant system developed, which effectively increased flushing and therefore potentially lead to a lower retention of larvae in such a system.

Understanding the transportation and retention of benthic marine larval is an essential first step for studying population connectivity in tidal lagoons (Cowen & Sponaugle, 2009, Levin, 2006, Shanks, 2009). During the pelagic larval life stage, the successful recruitment of benthic marine invertebrates is dependent on where and when transport occurs (Cowen and Sponaugle, 2009). Therefore, targeted management or conservation efforts are reliant on an understanding of local circulation patterns and transportation (Cowen et al. 2006, Levin 2006). As highlighted by my results, these processes may be complicated by several factors, such as complex localised morphology or release timing and location. These influences and the effect on transported benthic larvae potentially aid (or decrease) larval retention, and thus influence population connectivity. Within estuaries in which symmetrical circulation patterns are common or in systems with high flushing volumes, larval retention is expected to be low, and benthic populations would be reliant on recruits from other estuaries (Cowen & Sponaugle, 2009, Levin, 2006, Shanks, 2009). However, within estuaries such as Tauranga Harbour, where complex morphology (such as asymmetrical tidal channels, sand bars or estuarine islands) is present, retention may be increased. This increased retention is in addition to any larval behaviour, which may alter dispersal pathways (Herbert et al. 2012; North et al. 2008, Metaxas & Saunders 2009).

In recent decades, attention to transport and retention in marine systems has substantially increased in response to conservation and management of fisheries resources, spread of invasive species and the development of marine reserves (Levin 2006). In Tauranga Harbour reduced shellfish stocks such as *Austrovenus stutchburyi* and *Paphies australis* are increasingly of concern. Therefore, understanding the supply dynamics of these species, in particular the source regions/populations, is vital for successful management. As indicated by my results, larval dispersal and retention is largely controlled by the circulation patterns of the study area. Understanding how small scale morphologies influence the large scale circulation is critical for the success of invertebrate population management or conservation efforts. In Tauranga Harbour, it is clear that retention is increased within the upper estuary due to the extension of transport caused by small-scale morphological controls. Therefore, for the purposes of population management in this and other similar meso-tidal estuaries, focusing on the communities within the upper reaches of the harbour would be prudent.

Although care has been taken to limit sources of error within the field and modelling approaches, there are several limitations. There are larval samples within the main channels of the harbour, however no data are available for the sub-estuaries, and it is therefore difficult to confirm retention estimates within these areas. There is also relatively poor taxonomic resolution within the sampled data meaning that I cannot directly relate the water column larvae to benthic populations within regions of the harbour. It is also not possible to state with certainty that the taxa sampled at the different locations were the same species. With greater taxonomic resolution, I could link the water column samples to benthic populations within the harbour, providing calibration and validation data for use in connectivity based research. Considering that I have not included larval behaviour in my larval tracking model, my retention estimates have limitations. Larval behaviours that alter transport rates include but are not limited to diurnal migration, active or preferential settling or resuspension and vertical swimming. Although many benthic invertebrates have a low horizontal swimming ability, active vertical swimming can control their speed and direction of travel (Young 1995; Lundquist et al. 2004, Metaxas & Saunders, 2009). Within large systems (e.g. Chesapeake Bay or Poole Harbour), differences in water column salinity drive vertical swimming behaviours, actively increasing

internal larval retention (Herbert et al. 2012, North et al. 2008). Previous modelling efforts have included larvae with a vertical swimming ability (e.g. Herbert et al. 2012, North et al. 2008); however, as Tauranga Harbour has no or little stratification and observed larval distributions showed no depth variation (except for crab megalopae which made up a very low proportion (< 0.5 %) of the larval community), I did not include this. There is little available behaviour data for the larval stages of the species present within Tauranga Harbour (such as growth and mortality rates or larval behaviours), therefore the addition of behaviour would be difficult to validate. Given that I have selected neutrally buoyant particles, my results generally represent small larvae; older heavier larvae would need to be represented with negative buoyancy. To balance model accuracy and computation time, I have limited the model to one month for transport pathways to be interpreted and 16 days for retention estimates. This could be further extended to multiple years to interpret annual variation and for use with a greater range of benthic invertebrate species.

3.5. Conclusion

Benthic invertebrate population connectivity within estuaries that are well mixed, and often defined as well flushed, have been assumed to be primarily driven by recruits produced external to the estuary and/or larval behaviour (Caley et al. 1996; Cowen et al. 2006). However, complex morphological changes and controls at the scale of 10s to 100s of meters have generally not been considered or the influence of these on large scale circulation is under predicted. I have identified the importance of small scale changes in channel morphology across a transect (<1 km wide), where tidal flow is diverted and asymmetric circulation patterns are formed. From this flow diversion, larval transport is extended and retention is increased. This increased retention was obvious for modelled larvae released up-estuary of these morphological features, when compared to both seaward channel release and regions that are not influenced by these features. In harbour locations without these morphological controls, increased retention was driven by the timing of release and the direction of initial transport. From this I conclude that for population management or conservation, a focus on populations in the upper harbour, would result in an internal source of new recruits. Estuaries in which there are morphological controls (e.g. estuarine islands, complex channel morphology or

embayments) would also be expected to retain larvae in regions where the tides were most shaped by the landscape complexity. In areas that are not controlled by morphological features, retention can also be increased by timing and location of larval release (e.g. neap-tide vs spring tide, flood-tide vs ebb-tide and upper tidal flat vs in the channel).

Chapter 4. General discussion

Globally, coastal ecosystems are under increased stress from human activities (Jackson et al. 2001, Kemp et al. 2005, Levin, 2006, Cowen & Sponaugle, 2009). These stresses have in many cases lowered biodiversity and resilience in soft sediment, estuarine ecosystems through changes to nutrient and sedimentation regime, habitat losses, and the establishment of non-native species (Haywood, 1997, Thrush et al. 2006, 2008, Turner & Schwarz, 2006). It is well understood that benthic marine invertebrates within these soft sediment communities provide a number of key ecosystem services (e.g. water column filtration, nutrient cycling, and trophic transfer; Thrush et al. 2008, 2013). Biodiversity in these communities influences these ecosystem services and resilience to increased anthropogenic pressure (Thrush et al. 2006, 2017). Losses of a single species from a community can negatively affect the ability of soft sediment ecosystems to provide these functions (Thrush et al. 2006, 2017, Lohrer et al. 2010). Recovery following disturbance in soft sediment communities is dependent on the supply of new individuals (Underwood & Fairweather, 1989, Caley et al. 1996). Populations with external sources of new recruits (i.e. are open in terms of population connectivity), are better equipped to recover from disturbance (Cowen & Sponaugle, 2009, Thrush et al. 2008, 2013). The transfer of individuals between populations in soft sediment communities is controlled by dispersal by tidal circulation, local hydrodynamic conditions, such as residual circulation and coastal influences, such as coastal upwelling and tidal fronts (Cowen et al. 2006, Levin, 2006, Gawarkieicz et al. 2007, Cowen & Sponaugle, 2009).

In the past decade, there has been increased effort in understanding the dispersal of larvae in the marine environment due to population management and investigations of invasive species (Levin, 2006). As dispersal in marine invertebrates is generally limited to the pelagic larval stage (Cowen et al. 2006, Levin, 2006, Cowen & Sponaugle, 2009, Shanks, 2009), this life stage has been the focus for the estimation of dispersal. These studies have investigated dispersal with field collected data or bio-physical modelling investigations, with very few that have used a combination, other than for calibration purposes (see Tilberg et al. 2006 for an exception). I have successfully developed a calibrated 20 m resolution, hydrodynamic model and

coupled this to a larval tracking programme (Chapter 2). This coupled model was applied to aid the interpretation of a field data set that described the spatial and temporal variation of benthic invertebrate larvae (Chapter 3). My research provides further evidence that during this pelagic phase, dispersal of benthic invertebrate larvae is strongly controlled by local hydrodynamics (Chapter 3).

Chapter 3 highlights that a better understanding of the local hydrodynamics in large meso-tidal basins is needed to effectively manage and understand population connectivity in benthic marine communities. From the results that are described in Chapter 3, it is evident that there are asymmetric tidal flow patterns and retentive regions present in Tauranga Harbour, due to complex channel morphology (summarised in Figure 4-1). To my knowledge, there have been no earlier studies that have directly related morphological changes to increased larval retention. The larval community composition differences of the OM transect highlight the substantial variations that are possible across a transect of less than one kilometre due to the flow pathways caused these morphological differences (Figure 3-2 panel A). It also has not been shown that morphology on a scale of 10s to 100s of meters can significantly impact on the large-scale transportation pathways of an estuary. Recent studies have however identified the importance of local hydrodynamics and/or conditions, and the location and timing of release of larvae (Cowen et al. 2006, Jessopp & McAllen, 2008, Levin, 2006, Lundquist et al. 2004, Nickols et al. 2015). The influence of behaviour has also been highlighted in earlier studies (e.g. Herbert et al. 2012, North et al. 2008, Broekhuizen et al. 2011). As I have excluded behaviour from LTRANS simulations, larval retention is potentially underestimated or overestimated depending on the life history of the organism (for example, development of crab species occurs on the outer coast; Mense & Wenner, 1989). Analysis of the surface and bottom water column samples and a comparison during day and night collection of the February 1999 field campaign did not show any clear vertical migration in the taxa observed (Figure 2-2 & Figure 2-3). This observation highlights that the local scale hydrodynamic processes are potentially of greater importance than behavioural controls in this system; the addition of behaviour in numerical modelling efforts would confirm this hypothesis.

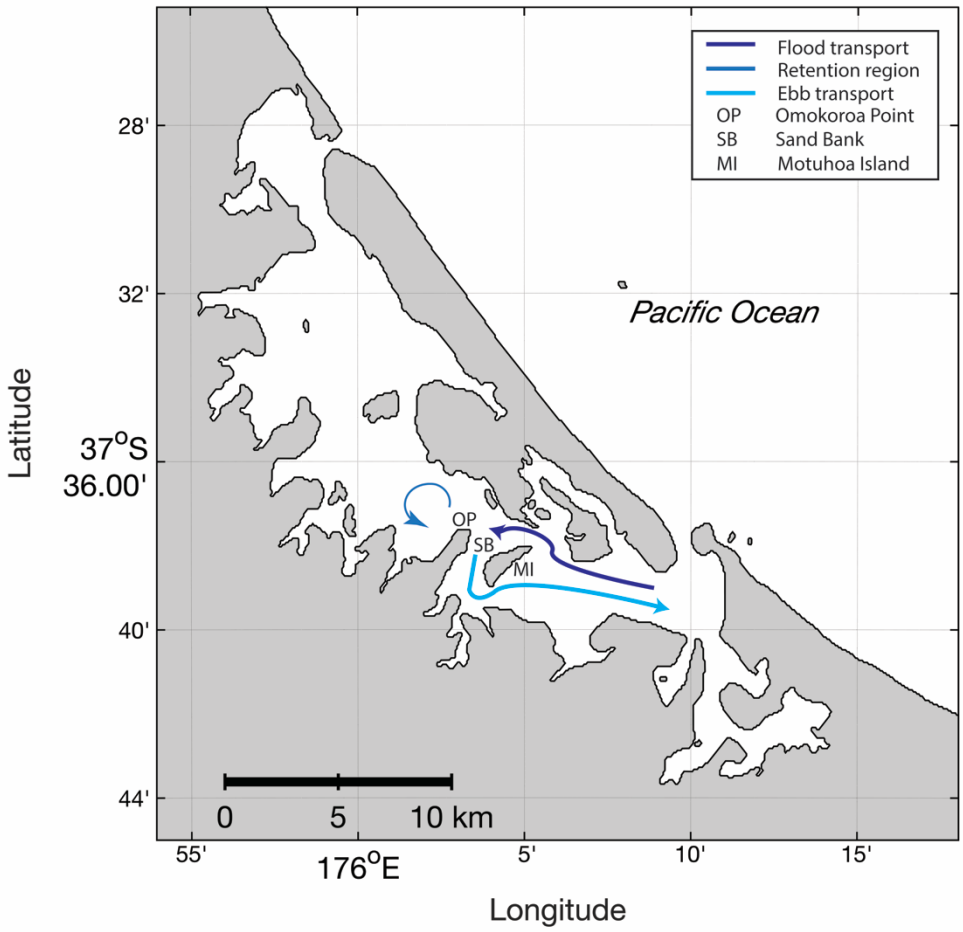

Figure 4-1: Summary of the dominant tidal and larval transportation pathways in the southern Tauranga Harbour. Flood and ebb asymmetry, the upper harbour retention region and locations of morphological controls (Omokoroa Point, Motuhoa Island and an intertidal sand bank) are identified.

My research provides details relevant to the spatial management of benthic marine invertebrate species in the southern Tauranga Harbour. Modelling results indicate that populations in the upper harbour region (above Omokoroa Point; Figure 4-1) may provide a source of new recruits to other harbour regions. Therefore, focusing on this region for population management and the protection of the morphological features that contribute to flow asymmetry and retention, may yield the greatest success for intra-estuary connectivity. There are several areas in Tauranga Harbour which contain culturally significant shellfish beds (e.g. Gouk, 2001, Ellis et al. 2013), including sandflats in the mid-harbour (near Motuhoa Island; Figure 4-1), near the Wairoa River mouth (Figure 3-1), and Centre Bank (Figure 3-1). Model results show that retention within the harbour for the mid-harbour and Wairoa sub-

estuary varies dependent on larval release timing, and retention of larvae released from the Centre Bank is low. Therefore, management of populations in the mid-harbour and Wairoa sub-estuary (and potentially other sub-regions of the harbour) will have variable success, and the spawning behaviour of the target species will be a significant influence (i.e. if spawning at low/flood tide, retention will be greater; however, if spawning occurs at high/ebb tide, larvae will be flushed from the harbour). The low retention of the Centre Bank simulations indicates that this region does not provide a source of recruits for intra-estuary connectivity. However, as the model assumes that larvae that reach the outer boundary are lost from the harbour, re-entry to the harbour is not possible. The life history of marine invertebrates varies between taxa and between species. For example, many crustacean species spawn in an estuary, the larvae are transported to the coastal region, where development to the juvenile stage occurs before re-entering into a estuarine ecosystem (Mense & Wenner, 1989). This thesis does not aim to capture life histories that include coastal or open ocean stages or inter-estuary dispersal. These transfers have potential risks to individuals finding suitable habitat, due to the occurrence of coastal features and systems.

As semi-enclosed meso-tidal lagoons are common estuary types, it is expected that complex and potentially small scale features in other coastal lagoons (e.g. the occurrence of sand banks, estuarine islands, and features that contribute to flow instabilities or divergence), may have similar impacts on harbour retention. This in harbour retention provides sources of individuals at the local scale, effectively increasing intra-estuary connectivity. This in harbour retention may aid the re-establishment of soft-sediment communities following disturbance, thus potentially increasing resilience to these disturbances. My research highlights that soft-sediment estuarine populations may not be as open as previously presumed, and larval transport and retention is greatly influenced by the local hydrodynamics.

4.1. Recommendations for future research

The use of a finer resolution hydrodynamic model than had previously been used to describe the tidal flows in Tauranga Harbour was successful in this study. Coupling of this hydrodynamic model to a larval tracking programme to aid the description of spatial and temporal variations in benthic invertebrate larval samples, successfully identified transportation pathways and retentive regions in the harbour.

However, there are several areas of improvement that would provide greater accuracy, and better understanding of population connectivity of soft-sediment communities. Improved spatial resolution of benthic invertebrate larval data, identified to species level is recommended in future population connectivity studies. It is now possible to identify benthic invertebrate larvae to species level using methods such as polymerase chain reaction (PCR; Coffroth & Mulawka, 1995) or DNA barcoding (Webb et al. 2006). Increased spatial and taxonomic resolution would improve understanding of dispersal from specific invertebrate patches and harbour regions. Laboratory based studies during the larval stage of common, local benthic invertebrate species are also recommended. These investigations could include larval growth and mortality (Metaxas & Saunders, 2009), vertical migration due to water column cues (Young, 1995, Metaxas, 2001) or behaviour during settlement (e.g. habitat preference, North et al. 2008, and sensory cues, Kingsford et al. 2002). The data collected could then be added to future bio-physical modelling efforts.

The hydrodynamic model successfully resolved the influence of morphological features on large scale circulation in the harbour. However, further grid refinement in these would improve accuracy. When I developed the grid used in this study, the flexible mesh modelling approach was not available in the open source Delft package. The availability of this package in future modelling will allow grid refinement in regions with strongly varying bathymetry across small spatial scales (e.g. in the sub-estuary channels, or at the Omokoroa point). To improve the bathymetric grid, additional depth data in the sub-tidal areas is also needed. The hydrodynamic model was not calibrated for the sub-estuaries; therefore, it is not possible to comment on the accuracy of the model in these areas. To accurately investigate the population connectivity in Tauranga Harbour, it is recommended that calibration data is collected and applied in these regions. Additionally, investigations in other similar meso-tidal estuaries would confirm if the effect of small scale (10s to 100s of meters) morphology impacts on circulation, are common.

Dispersal curves and dispersal kernels are often calculated in the investigation of population connectivity (Moilenan & Niemanen, 2002, Cowen et al. 2006, Cowen et al. 2007, Paris et al. 2007). This method requires multiple bio-physical

simulations which release larvae from known target species populations, tracking during the pelagic phase and include growth and settlement (e.g. Cowen et al. 2006, 2009, Siegel et al. 2003). The output from these analyses provide the distance of dispersal and the probability of transfer between populations, and indicate how 'open' or 'closed' a population is. Future studies would therefore benefit from the estimation of dispersal kernels to investigate population connectivity. In addition to local transfer (i.e. within estuary), regional scale investigations would confirm if intra- or inter-estuary connectivity is of greater importance to population persistence.

An investigation of how anthropogenic harbour modifications (e.g. channel dredging and land reclamation) alter larval dispersal, may provide insight into population dynamics pre- and post-development. This could be done by comparing the current population connectivity to the predicted pre-development dispersal. There is anecdotal evidence for previous harvesting locations of common, culturally significant shellfish species, and pre-development bathymetry available to aid such a study (see Brannigan, 2009 for changes to harbour entrance). From this analysis, conclusions could be made into the main driving forces for population decline and provide information into where management or reestablishment would be beneficial.

4.2. Conclusion

Human changes to estuarine ecosystems continue to place increasing stress to soft-sediment communities. The ability of these communities to recover or adapt to disturbance of these stresses is dependent on receiving new recruits from source populations. Therefore, understanding of the local dispersal characteristics is essential to better manage these populations. Local scale hydrodynamics in meso-tidal coastal lagoons can be strongly influenced by complex morphology. Variation in these morphologies at a scale of 10s or 100s of metres can strongly influence large scale tidal circulation in estuaries. Larval dispersal during the larval stage of benthic invertebrates is driven by regional and local scale hydrodynamics, and therefore can be influenced by morphological features. The application of field data analysis, together with coupled hydrodynamic-transport models provide useful tools to investigate larval dispersal in estuaries; provided that the scale at which these investigations are made is fine enough to observe these variations.

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